ECOLOGICAL PATTERNS OF THE SMALL MAMMAL COMMUNITIES AT EL CIELO BIOSPHERE RESERVE, TAMAULIPAS, MEXICO

A Dissertation

by

IVAN CASTRO-ARELLANO

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2005

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Thomas E. Lacher, Jr.
Committee Members,	Rodney L. Honeycutt
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ABSTRACT

Ecological Patterns of the Small Mammal Communities at El Cielo Biosphere Reserve, Tamaulipas, Mexico. (December 2005)

Ivan Castro-Arellano, B.S., National Autonomous University of Mexico; M.S., Texas A&M University

Chair of Advisory Committee: Dr. Thomas E. Lacher, Jr.

Scarce knowledge of Neotropical small mammal communities prevents experimental inquiry on the mechanisms structuring these communities. In this study, I examined patterns of local assembly of the small mammal communities on the eastern slopes of El Cielo Biosphere Reserve (ECBR) in Tamaulipas, Mexico, at two spatial scales. At the landscape level I tested patterns of species co-occurrences between four sites with a null model. At the local level I addressed floor microhabitat use, vertical structure use and temporal partitioning. I studied these niche axes at two adjoining forest types, Tropical Subdeciduous Forest (TSDF) and Cloud Forest (CF), that had different structural complexity. Total trapping effort consisted of 19,712 trapnights distributed over three years. In 1,365 capture events I recorded 789 individuals representing 14 species. Abundant species, mostly *Peromyscus* species that are of intermediate body size, co-occurred less often than expected by chance, whereas rare species, mainly *Reithrodontomys* species of small size, occurred at random over study sites. This pattern suggests that species interactions might be responsible for this non-

random structure. Both the TSDF and CF had striking differences in both microhabitat use and temporal partitioning. In the TSDF common species (>8 individuals) organized along a microhabitat gradient from grassy/open areas to closed forest areas. Temporal partitioning for the whole community was less than expected by chance with use of an ad hoc null model. Species from ecotone/open areas avoided use of middle portions of the night whereas the single forest species concentrated activity in this period. So, it is plausible that predator avoidance strategies might have higher impact on temporal partitioning as compared to competitive interactions. In high contrast the CF community was codominated by two *Peromyscus* species that overlapped heavily in both their microhabitat use and diel activity patterns. Ecological separation of these two species probably occurs along a niche axis not considered in my study or might be facilitated by their body mass difference. Overall, I provide the first account of community patterns for small mammals at ECBR. These patterns can provide the basis for experimental manipulations to ascertain mechanisms responsible for structure at these communities.

DEDICATION

To the memory of Mom and to my Dad

To my beloved wife who has endured
and supported my interest in ecology
and nature.

To Alfredito and Rosarito.
I hope that ideas and work from me
and all fellow ecologists will make
a difference for the world of your
children and grandchildren.

ACKNOWLEDGEMENTS

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learn many things from him. Dr. Rodney Honeycutt provided me access to his molecular genetics laboratory to do the species identifications and helped me fine-tune a field key to identify rodent species in the field. Most importantly, he gave me the opportunity to teach the laboratory for the mammalogy class he teaches at TAMU. This experience opened my eyes to the role and responsibilities of a mentor and obligated me to learn more about the fascinating biology of mammals. Dr. A. Harlin and Dr. H. Lopez-Fernandez, showed me the intricacies of basic molecular work and spent several hours each helping me out with the species identification process of my samples.

I also thank the facilities provided by the UAT-IEA for the use of Los Cedros biology field station. The Direccion General de Recursos Naturales y Medio Ambiente from Tamaulipas authorized the research permit to work at El Cielo Biosphere Reserve and the Direccion General de Vida Silvestre provided federal collecting permits.

During my time as a graduate student at TAMU, I had the opportunity to meet many fellow students: April Harlin, Dawn Sherry, Rob Powell, Melissa Parker, Mike Goldstein, Scott Brandes, Deborah Cowman, Maggie Mieres, Paco Ollervides, Hernan Lopez-Fernandez, Gage Dayton, J. V. Montoya, John Aguiar, Glen Proudfoot, Larry Frabotta, Collen I., Ryan Toby and many others. Each one helped me in one way or another and made life as a graduate student more enjoyable. I was very lucky to share a "bachelor's apartment" with Hernan Lopez-Fernandez because I not only learned a lot about phylogenies but also always had someone to share beer and tequila over profound ecological discussions!

I thank my dissertation committee: Drs. Thomas Lacher, Jr., Rodney Honeycutt, Ben Wu and Kirk Winemiller. Each one contributed towards my academic development not only through the classes I took with them but also with their comments and observations on my study. I especially want to acknowledge the support, guidance and intellectual challenges of my committee chair, Dr. Thomas Lacher, Jr. He was always there to provide ideas and encouragement to my work.

I also want to recognize the long-term support from my parents and brother. Without the early support of my parents I would have never reached my present goal. They always helped me develop my early interest in biology. The camping trips that I shared with my father and grandfather at a very young age instilled a love for the outdoors and motivated me to pursue a career in ecology.

Last, but not least, I must thank my loving wife whom I had the joy to met at TAMU. She not only emotionally supported me all the way through my research but also was always available to discuss statistical issues as well. She also wrote the software program that made possible to test an ad hoc null model for the temporal partitioning chapter. But her greatest gifts to me have been our son, Alfredito and our daughter, Rosarito. The three of them are my greatest joy and I consider myself the luckiest to have them as my family.

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CHAPTER I

INTRODUCTION: SMALL MAMMAL COMMUNITY ORGANIZATION

An understanding of mechanisms that determine species composition in ecological communities has been long sought by ecologists. Emphasis on community structure traces back to the early debate between Gleason (1926) and Clements (1916), who presented opposing views on plant community organization. Clemens (1916) treated assemblages as an integrated whole, regarding communities as "complex organisms" that eventually reach a climax state. On the contrary, Gleason (1926) argued that plant associations are the result of chance, dispersal mechanisms, and ever-changing environmental characteristics (Kingsland 1991). "Clementsian" communities are more dominated by competition, whereas "Gleasonian" assemblages are more a result of dispersal characteristics of species. While the strict Clementsian view lacks support today, both views represent milestones in theoretical ecology, and debate over these views promoted research on species composition in ecological communities. Recently, Hubbell (2001) renamed these two views as the niche-assembly and the dispersal-assembly perspectives. The niche-assembly concept considers communities as groups of interacting species, whose inclusion in the assemblage can be deduced from assembly rules that are based on each species' ecological niche. In contrast, the dispersal-assembly perspective considers communities as open systems with species included by a

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This dissertation follows the style and format of Journal of Mammalogy.

combination of chance, history, and random dispersal. Hubbell (2001) argues that debate over both concepts has persisted because each explanation is partially correct, and that reconciling these perspectives is "one of the most fundamental problems in ecology today" (Hubbell 2001: 26). Hubbell's neutral theory of ecology is a major attempt towards encompassing a synthetic theory that reconciles both perspectives. Nevertheless, some authors do not consider this theory to provide a definitive answer (Enquist et al. 2002; Gaston and Chown 2005). Debate over these issues in on-going, and research designed to investigate factors responsible for structure in ecological communities remains a priority. Small mammal communities provide excellent models for testing predictions of both the niche-assembly and dispersal assembly hypothesis. Considerable research on desert rodent communities has revealed highly structured assemblages (Dayan and Simberloff 1994; Heske et al. 1994; Kelt et al. 1995; Scott and Dunstone 2000; Jones et al. 2001), with competition playing an important role between some pairs of species (Brown and Harney 1993; Kronfeld-Schor and Dayan 1999). However, studies of rodent assemblages in the Texas coastal prairie, yet exploitation competition has not been found to be a dynamic force structuring these communities (Cameron 1977; Cameron et al. 1979; Kincaid and Cameron 1982). Instead, they are primarily the result of habitat selection, rather than being driven by competition (Kincaid et al. 1983). The same observation was made with similar species occurring in the post oak savanna habitat in east-central Texas (Turner and Grant 1987). These contrasting results clearly exemplify the most pervasive debate in community ecology is the one that pertains to the role of competition as the major force structuring communities.

Historically, competition has been at the center of discussion about the mechanisms responsible for the structure and dynamics of ecological communities (Brown et al. 2000). Not all researchers agree that competition is the major force structuring communities, because it is easily envisioned that species might utilize different sets of resources even in the absence of other species. One of the criticisms of early studies on patterns of resource partitioning was their failure to distinguish patterns of community structure resulting from either competition or chance (Chase and Liebold 2003). This is clearly an observation that applies to any study of resource partitioning, independently of what the presumed mechanism is behind the observed pattern. Currently, the simple demonstration of segregation in resource use is not accepted as direct evidence for competition, or any other mechanism responsible for that pattern.

The first step towards understanding community structure is to validate the observed pattern. Null models have been increasingly used to determine the extent of overlap in resource use expected in the absence of species interactions like competition (Gotelli and Graves 1996). This analytical approach provides a means to incorporate more rigor in ecological studies. Nevertheless, the increase of more sophisticated analytical approaches resulted in debate over the best approach to employ (Sanderson et al. 1998; Gotelli 2000; Gotelli and Entsminger 2001; Manly and Sanderson 2002; Gotelli and Entsminger 2003). Nevertheless, a well-designed null model that retains most of the characteristics of real communities, while randomizing factors to be examined, can be very enlightening since it provides a quantitative test of non-random resource use. However, very few communities have been tested with this kind of approach. Resource

partitioning by sympatric species and its role in allowing their coexistence are two basic questions in community ecology and both are amenable to testing with null models. It should be noted, however, that this analysis will not provide support to any specific mechanism responsible for the observed pattern (Sanderson 2004). Natural history studies and experimental manipulations are needed to ascertain the ultimate causation.

Regardless of geographic region, most studies of rodents have focused on diet and comparisons of microhabitat overlap (Emmons 1980; Kincaid et al. 1983; Dueser and Porter 1986; Lacher and Alho 1989; Gonnet and Ojeda 1998; Kronfeld-Schor and Dayan 1999; Jones et al. 2001; Lacher and Alho 2001), whereas few have considered factors such as species morphology (Smartt 1978; Dayan and Simberloff 1994; Ben Moshe et al. 2001), activity patterns (Ziv et al. 1993; Vieira and Baumgarten 1995; Kronfeld-Schor et al. 2001), and geographic origin (Kelt et al. 1995). Although microhabitat, diet and temporal niche axes are presumably responsible for most of the differentiation (Schoener 1974), they are seldom examined simultaneously. Furthermore, studies that have included these three niche axes have mostly examined simple habitats with little vertical structure (eg., deserts, prairie, savannas) and rodents belonging to a single guild (i.e., granivores). Because tropical habitats accommodate new species by guild expansion and/or creation of a new microhabitat axis (Emmons 1980; August 1983; Winemiller 1991), they can harbor more complex communities that observed in desert and temperate habitats.

Rigorous comparative studies of community structure in temperate and tropical communities should provide insights of possible processes responsible for these patterns

(Lacher and Mares 1986). However, comparisons between widely separated sites are complicated by profound historical and phylogenetic differences. A possible solution is to compare closely located sites that still reflect differences between temperate and tropical zones. Such a site occurs on northeastern Mexico at El Cielo Biosphere Reserve (ECBR). This site represents a zone of convergence between tropical and temperate biomes. The reserve encompasses an altitudinal gradient with adjacent vegetation types biogeographically related to either Neartic (Miranda and Sharp 1950; Martin and Harrel 1957) or Neotropical zones (Valiente-Banuet et al. 1995).

Herein a comparative study of the small mammal communities at two distinct sites at ECBR is presented. This study encompassed two different niche axes, and considered impingement of processes occurring at larger scales (i.e., landscape level) are examined. I specifically addressed the patterns of co-occurrence at the landscape level (Chapter II) as well as temporal (Chapter III) and microhabitat (Chapter IV) partitioning between species at the local level. Independent of the specific studies presented in each chapter, I addressed two general hypotheses including: 1) The expectation of the occurrence of more generalists and wider niche overlaps in temperate-derived communities and more specialists and less niche overlap in tropical-derived communities; 2) Different niche partitioning, between species pairs when moe than one dimension of niche space is examined. Since complementation allows for coexistence of more species at a site, I expect it to be more prevalent in the tropical-related communities.

My tests of observed patterns do not confirm a specific process (eg., competition). Rather, this study should be viewed as a useful starting point for the development of hypothesis and the identification of subsets of species and factors that can be subjected to experimental analysis, thus allowing for the ascertainment of mechanisms responsible for the observed patterns. Very little is known for both the level of whole assemblage and the level of individual species at these sites. Therefore, the contribution of this study on knowledge of this unique area of Mexico promises to be positive.

CHAPTER II

LANDSCAPE CO-OCCURRENCE PATTERNS OF RODENT SPECIES AT EL CIELO RESERVE

The study of elevational gradients holds a distinguished historical position in the development of biogeography and ecology (Lomolino 2001). The last decade has seen an increased interest in elevational studies accompanied by a fundamental shift in the approach by which these diversity patterns are addressed (Rahbek 1995). Studies of elevational gradients have concentrated mostly on analyzing patterns of species richness distributions along these gradients (Rahbek 1997; Lomolino 2001). Studies addressing this issue have been done for a variety of taxa including small mammals (Rickart et al. 1991; Patterson et al. 1998; Shepherd and Kelt 1999; Heaney 2001). The original perception was that diversity along elevational gradients decreased monotonically with increasing elevation, but this notion was based on few studies (Terborgh 1977). A later literature review found that this monotonic curve of diversity was less prevalent than a more widespread pattern where species numbers exhibited a hump-shape with highest diversity at mid-elevations (Rahbek 1995). A proposed null model, the mid-domain effect, predicted these mid-elevational peaks in diversity based upon spatial constraints of species range placement between mountain tops and coastlines (Colwell and Hurtt 1994; Colwell and Lees 2000; McCain 2004). This null model approach, although contested (Zapata et al. 2003), has nevertheless provided new insights on this species diversity pattern by providing a strict analytical approach (Veech 2000; Colwell et al.

2004; McCain 2005). Compared to the vast body of research about species diversity patterns, the effort dedicated to elucidate community structure patterns along elevational and other environmental gradients has been more limited. The early work of Whittaker (1967) provided the theoretical and practical grounds to develop a research paradigm aimed at elucidating the structure of communities along gradients. Working on plant communities, he portrayed models for the organization of assemblages along gradients on the basis of whether or not species occur in recognizable groupings and the extent to which boundaries between species were exclusive (Whittaker 1967). Other researchers have later attempted to identify mechanisms organizing communities along gradients (Terborgh and Weske 1975; Whittaker and Niering 1975; Terborgh 1985; Mac Nally 1990). One recent study introduced a novel approach by using null model tests of the patterns of species range boundaries and abundances for the herpetofaunal assemblages at Mount Kupe (900-200 m) in Cameroon (Hofer et al. 1999). These authors found that observed patterns did not differ from random expectations for the whole assemblage. However, when their original data were re-analyzed with a different null model, that encompassed a more appropriate null space significant differences from random pattern became evident (Sanderson 2004). This later null model was based on species occurrences instead of range boundaries, and borrowed from the ideas used to analyze bird species distributions on islands. Around the time Whittaker's research about community organization on gradients was being developed, another paradigm about the co-occurrence of species on islands was initiated (Diamond 1975). This seminal work suggested that island bird community structure can be explained by assembly rules

determined by competitive interactions and has had a profound impact on community ecology (Weiher and Keddy 1999). This paradigm has been addressed extensively with null model analyses (Gotelli 2000) and now it has been shown that both the methods and the island paradigm have wider applicability in the analysis of species co-occurrences over gradients (Sanderson 2004).

No study of co-occurrence patterns of small mammals over elevational gradients has been conducted, even though more than 50 studies concerning species diversity along elevational gradients have been documented on a global scale for this group (McCain 2005). The models to analyze community structure along these environmental gradients are well developed but have not been applied broadly (Gotelli and Graves 1996).

In the present chapter I make use of null model tests to analyze the species distribution patterns of a rodent assemblage from the east-facing slope of El Cielo Biosphere Reserve in Tamaulipas, Mexico. Since the use of a single model has a higher potential of biasing conclusions (Gotelli and Graves 1996), I used different simulations of increasing complexity to address the structure of these assemblages. Specifically, I test the null hypothesis of random species co-occurrences among the vegetation types occurring in this zone.

MATERIALS AND METHODS

Study area.— El Cielo Biosphere Reserve (ECBR) is a conservation zone of approximately 144, 500 ha located in southwestern Tamaulipas, Mexico, that forms part

of the Man and the Biosphere system of UNESCO (Figure 1). This highly heterogeneous region of the Sierra Madre Oriental is a transitional zone where tropical elements coexist with those of temperate origins. To the east the ECBR is bordered by the Gulf Coastal Plain, which extends to 200 meters in elevation (Figure 2). From this point to the west the sierra raises rapidly to a plateau located between 900 and 1,200 meters. Continuing westward, a second slope gives raise to a higher plateau (1,900-2,100 meters) that then descends into a series of hills and valleys that end at the Mexican Central Plateau (Martin 1955; Sosa 1987). In a straight east-west line of only 21 Km, a vegetation gradient goes from tropical to temperate and xerophitic associations (Sosa 1987). Within the reserve, four major vegetation zones exist (Figure 3): Tropical Subdeciduous Forest (TSDF), Cloud Forest (CF), Pine-Oak Forest (POF) and Xerophitic Scrub (XS). On the eastern side of ECBR, the Coastal Plain Vegetation (CPV) has been greatly modified into an agricultural landscape where sugarcane, citrus and cattle ranching activities have left only a few remnants from the original vegetation cover. The fieldwork for my study was conducted in the southeast portion of the Reserve within the limits of Gomez Farias municipality (23 03'42" N and 99 12'18" W). I sampled four areas that covered most of the altitudinal gradient on the eastern slope of this portion of the ECBR. In related studies (Chapter III and IV), I intensively trapped at TSDF and CF sites in order to document the microhabitat and temporal niche partitioning at these rodent communities. Average altitude for the TSDF sites was 300 meters, whereas CF sites were located around 1,300 meters. Capture data from those studies was used for analyses in the present study together with the information obtained from additional

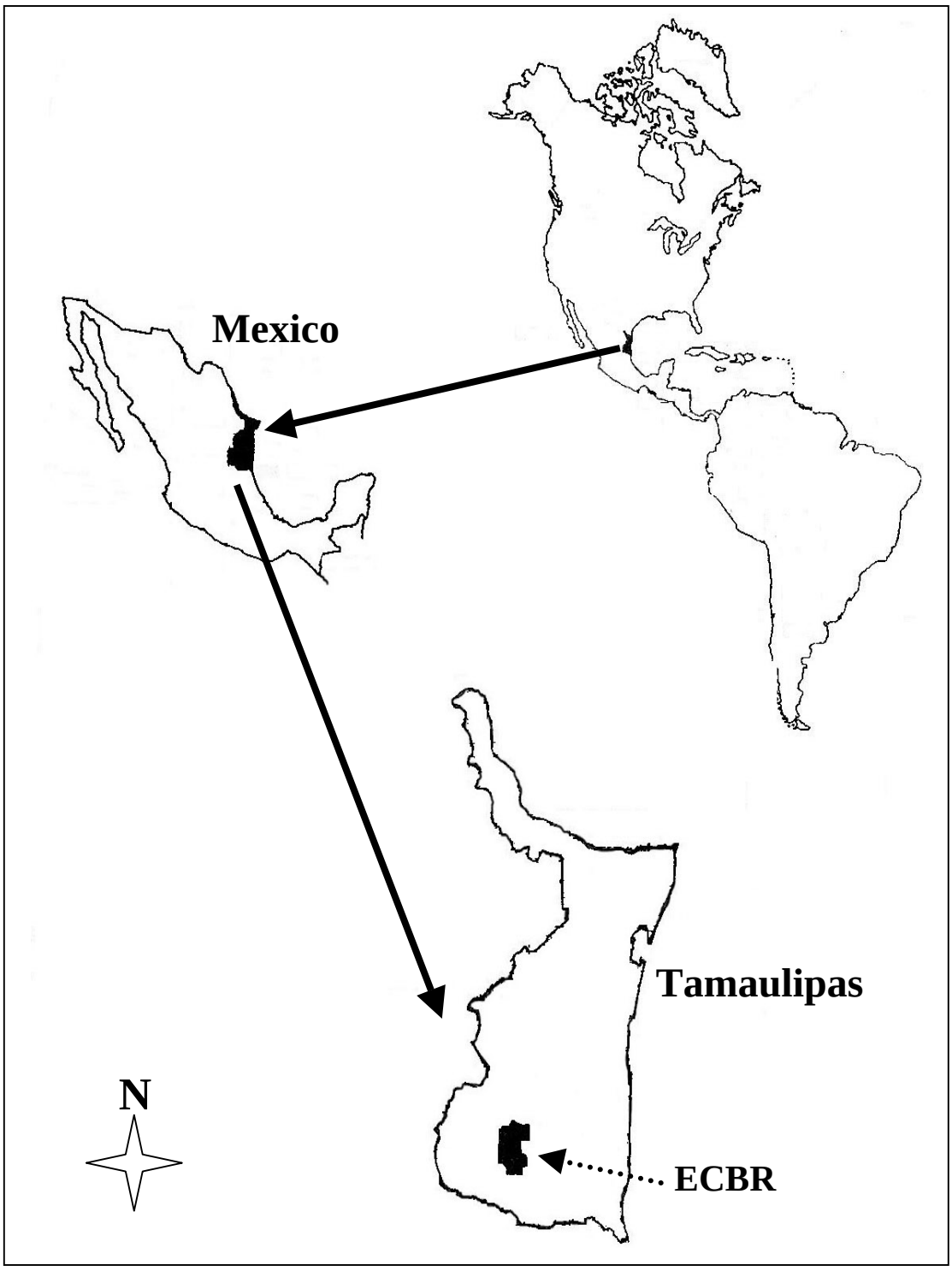

Figure 1.—Location of El Cielo Biosphere Reserve in Tamaulipas, Mexico.

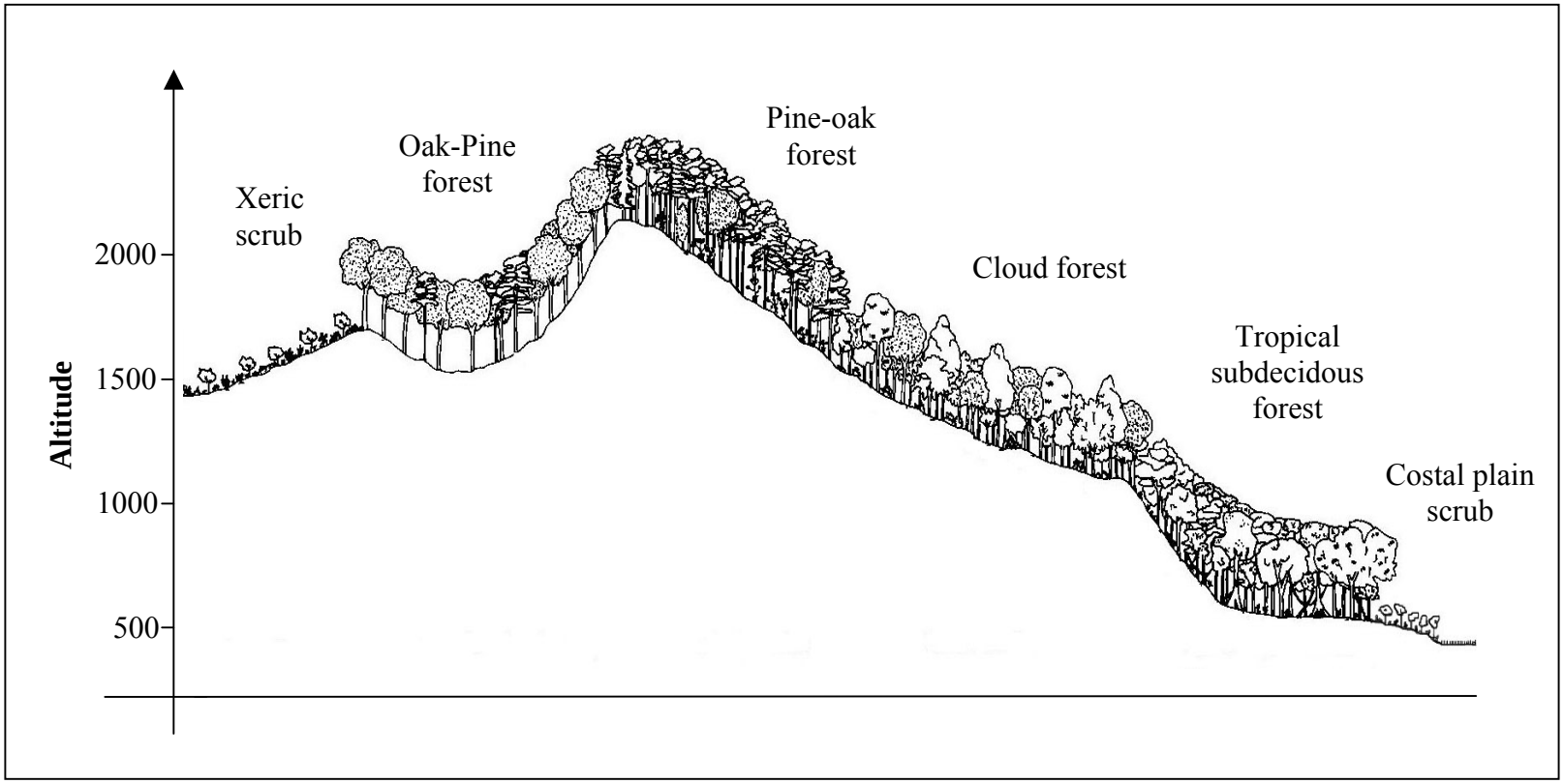

Figure 2.—Diagram of the elevational gradient and distribution of vegetation types over the eastern facing slopes of El Cielo Biosphere Reserve.

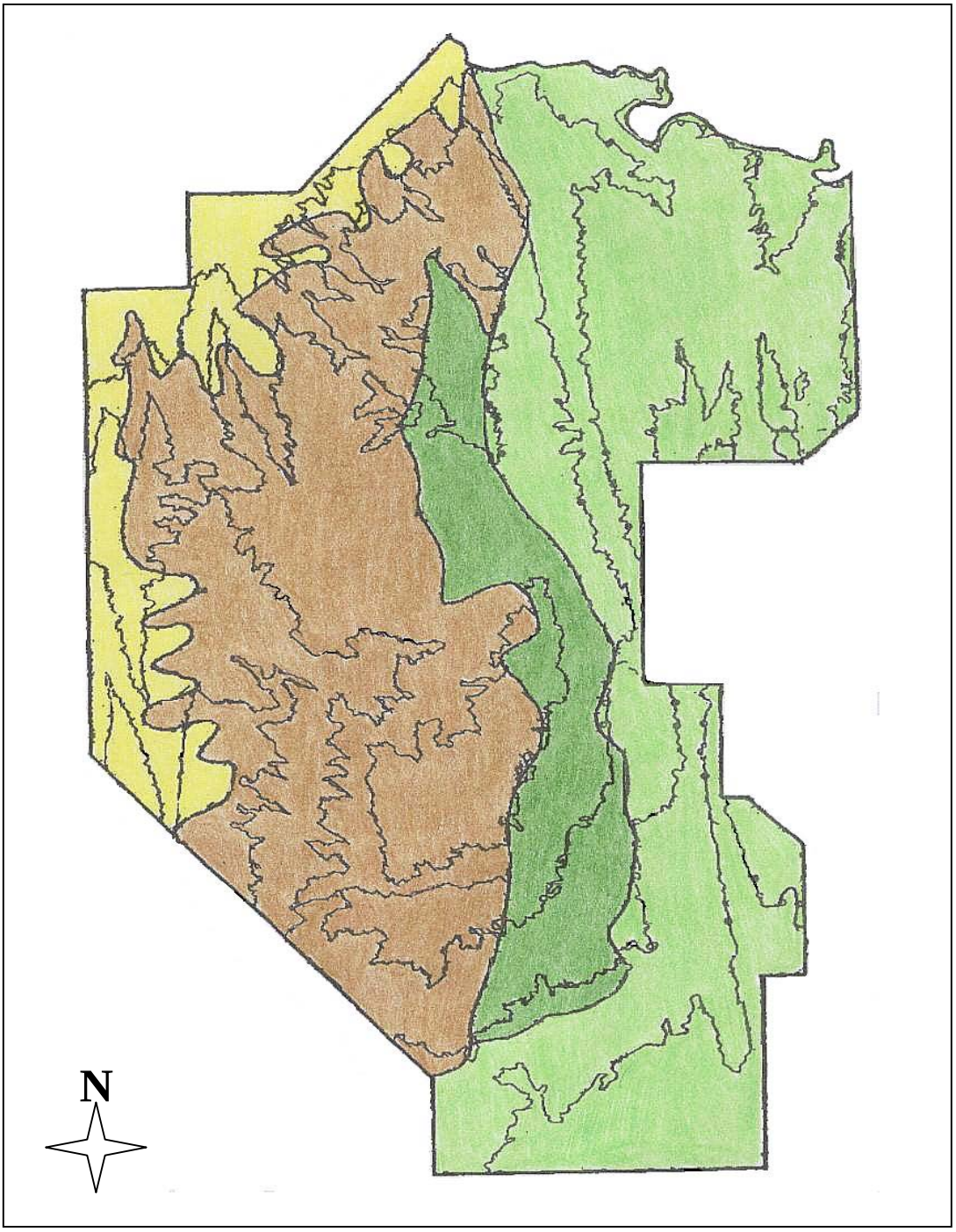

Figure 3.—Diagram of the distribution for the four major vegetation types within El Cielo Biosphere Reserve. Tropical Subdeciduous Forest (Light green), Cloud Forest (dark green), Pine-Oak Forest (Brown) and Xerophitic Scrub (yellow).

trapping sessions I conducted at two other zones, one located at the TSDF - CF transition and another at a private ranch on the eastern border of the reserve. The ecotone between CF and TSDF is not sharply defined, taking place at a zone between 800 and 1,100 meters that has a mix of dominant plant species from both vegetation types (Puig et al. 1987). The transition sites (TS) I sampled at this zone were located at 900 meters in the vicinity of Alta Cimas locality. Finally, samples from the CPV came from sites with an altitude of 90 meters and were contained in a ranch located approximately 2 Km from the reserve border. The owner of this ranch has preserved some large areas of natural vegetation in an otherwise agriculturally modified zone.

Trapping design.— I did fieldwork during the summer months, May to August, of 2001, 2002 and 2003. At the TSDF and CF vegetation zones, I used four different sites to sample each rodent community, whereas sampling at the TS and the CPV consisted on two sites each. For each trapping session at a site, I established one Sherman live trap transect of 150 to 180 traps set 7 mts apart and baited with peanut butter, rolled oats and vanilla extract. Transects were active from three to six nights in a row with traps set by 1900 hr and checked usually until the next day. Captured individuals were identified, weighted, sexed, marked and released at their capture sites. For the present study, I pooled capture information from collecting sites of each vegetation type to obtain a species list for each one. Overall, I completed a total of 19,712 night traps that represent the sampling effort for this study. Since I will compare species presence-patterns between vegetation types, it is crucial to determine if each community has been adequately sampled. There are many approaches for the

measurement of species richness in a community, with the effects of abundance and sampling effort being important to establish adequate comparisons (Colwell and Coddington 1994; Gotelli and Colwell 2001). I used species accumulation functions to assess survey completeness in each vegetation type (Soberon and Llorente 1993; Colwell and Coddington 1994). A species accumulation function is a curve that represents the expected accumulated number of species within an area as a function of a measure of collecting effort. I used the Species Accumulation Functions (SAF) freeware application (Diaz-Frances and Soberon 2005) to fit and select the best model between three widely used species accumulation functions for each vegetation dataset (Soberon and Llorente 1993; Diaz-Frances and Gorostiza 2002). During fieldwork, I collected a representative set of individuals coming from all sites that I prepared as voucher specimens. Vouchers are deposited at the Texas Cooperative Wildlife Collection (TCWC), Texas A&M University and Museo de Historia Natural de Tamaulipas in Ciudad Victoria Tamaulipas. Since a specific key for the small mammals of this area is not available, I identified specimens with the aid of several sources (Cameron and Spencer 1981; Hall 1981; Lackey et al. 1985; Eshelman and Cameron 1987; Davis and Schmidly 1994; Reid 1997; Villa and Cervantes 2003) and with comparisons of reference specimens deposited at the TCWC. For two species of the genus *Peromyscus,* I used an additional method of identification based on cranial features of collected specimens (Modi 1978; Schmidly 1972) as well as comparison of cytochrome *b* sequences to reference material.

Genetic species identification. — Four species of the genus *Peromyscus* are known to occur at ECBR. Two of these, *Peromyscus ochraventer* and *Peromyscus*

leucopus, are easily recognized since the former is a large species with an striking ventral zone of an ochre coloration, unusual for this genus, and the later is a small species with a very white ventral zone (Lackey et al. 1985; Villa and Cervantes 2003). However, the other species pair, *Peromyscus pectoralis* and *Peromyscus levipes*, overlap in several of their external characteristics, and some individuals can only be differentiated with detailed quantitative analyses of skull features and baculum characteristics (Hooper 1952; Schmidly 1972; Schmidly and Hendricks 1984), thus requiring that each individual is killed and kept as a specimen for correct identification. Also, morphological analyses of skulls for species identification can only be applied to adult individuals with juveniles being impossible to separate by this method. So, given the limitations in numbers of individuals that could be collected by both local and federal permits, the need to release these rodents for purposes of other study objectives (Chapter III and IV), and the presence of many juvenile individuals in my sampling, I resorted to genetic identifications of captured individuals.

For every captured individual I preserved a 2 mm tail clip, in either 70% ethanol or in a 20% DMSO saturated salt solution. The entire mitochondrial cytochrome *b* gene (1140 base pairs) was analyzed and compared to reference sequences from published material (Bradley et al. 2000; Tiemann-Boege et al. 2000). Mitochondrial DNA was extracted from tail clip samples using the DNeasy Tissue Kit (Qiagen, Valencia, CA). For all samples the cytochrome *b* gene was amplified via the polymerase chain reaction (Saiki et al. 1989) using the following parameters: 35 cycles of 94 ºC (30 s) denaturing, 50 ºC (1 min) annealing and 72 ºC (1 min, 10 s) extension; followed by one cycle of

72ºC (4 mins). Amplification reactions were performed in 50 µl volumes, 10 mM Tris-Cl, 50 mM KCl, 2 mM MgCl2, 1 µM primer concentration, and 1.25 U of Taq (Fisher Scientific, Pittsburgh, PA). A combination of primers (See Appendix I) was used to obtain amplification products of the cytochrome *b* gene (Bradley et al. 2000). Amplified products were purified with an enzymatic procedure (EXOSAP, USB Scientific) enzyme cleanup. Amplicons were sequenced with fluorescent-labeled dideoxynucleotide terminators (BigDye, Applied Biosystems, Foster City, CA) following the manufacture's protocol and the primers used for amplification. Unincorporated fluorescent primers were removed with a Sephadex spin column procedure (Sigma Aldrich Corp.). Sequencing was performed in an automated ABI Prism 377 or 3100 automated sequencer (Applied Biosystems, Foster City, CA). Nucleotide sequences were aligned and edited using the software Sequencher (Version 4.2.2, Genes Code Corporation, Ann Arbor, Michigan). Phylogenetic affinities, and thus specific identifications, were ascertained by phylogenetic analysis of sequences from captured individuals and published sequences of *P. pectoralis* and *P. levipes* obtained from GenBank (See Appendix I) using PAUP (Swofford 2002).

Null model analyses.— To address the structure of species co-occurrences over the gradient of ECBR, I used two original datasets (Appendix II): one from my fieldwork sampling and another from a published work listing known species occurrences at each major vegetation type from ECBR (Vargas-Contreras and Hernandez-Huerta 2001). Since both datasets do not overlap totally in their vegetation type coverage, I also created a restricted version from this last dataset so that only

species in common between both datasets are considered. I excluded introduced species records from my dataset and did not include completely fossorial (Geomyidae) and diurnal-arboreal (Sciuridae) rodents from Vargas-Contreras and Hernandez-Huerta dataset, since they represent completely different guilds to the terrestrial-nocturnal rodents that I trapped. Null model procedures followed the steps of classical randomization tests: Information from each dataset is organized as a presence-absence matrix in which each column represents a site (ie., vegetation type) and each row represents a species. Entries in the matrix indicate the presence (1) or absence (0) of a particular species at a particular site. After data are randomized with a defined algorithm, an index that describes the co-occurrence pattern as a single number is calculated and the process is repeated many times (10,000 for the present study). The frequency distribution thus created is used to test the null hypothesis that the value of the index for observed data was drawn at random from this distribution (Gotelli 2000). For all simulations I used two different indices to measure species co-occurrences. The first one is number of checkerboard species pairs (CHECK) which corresponds to the number of species pairs that form a perfect checkerboard, ie., they never co-occur in any site, thus representing the strongest pattern of species repulsion (Diamond 1975; Gotelli and Graves 1996); and the second one is the "checkerboardedness" index, or C-score, that measures the average amount of co-occurrence among all unique species pairs (Stone and Roberts 1990). For both indices, significantly higher values than expected by chance mean there is a pattern of species segregation higher than would be expected just by random species sorting among the vegetation types.

I used Monte Carlo simulations to randomize each data matrix using Ecosim 7.0 simulation software (Gotelli and Entsminger 2004). This software provides up to 36 standard simulation variations plus the capability of assigning independent weights for either sites or species thus allowing a powerful exploration of data by altering model assumptions. However, a systematic study of the performance of each simulation algorithm against matrices of known structure has shown that some of these variations are prone to either Type I error (false positives) or Type II error (false negatives) thus actually reducing the number of simulations that can be used effectively (Gotelli 2000). Based on the results from Gotelli (2000) I selected two of the standard (non-weighted) simulations that have shown good performance for detecting non-random patterns, and also I included two simulations using independent species weights for analysis of each dataset. I maintained the simulation names used by Gotelli (2000) for non-weighted standard simulations. Algorithm explanations for each simulation are as follows:

Simulation 2 (SIM2): Fixed rows-Equiprobable columns. In this simulation the observed row totals are maintained, ie., number of occurrences of each species in the null communities is the same as in the original dataset, but each column, or site, is equally likely to be represented. This simulation has already been used before for community ecology analyses (Winemiller and Pianka 1990; Inger and Colwell 2005).

Simulation 9 (SIM9): Fixed rows-Fixed columns. This simulation maintains fixed rows and columns sums. So, both the total number of occurrences of each species and the total number of species at each site in the simulations

are the same as in the original dataset. Since selection of the adequate algorithm for this simulation has been contentious since the first time it was used to test species co-occurrences (Connor and Simberloff 1979; Connor and Simberloff 1984; Diamond and Gilpin 1982; Manly 1995; Sanderson et al 1998; Gotelli and Entsminger 2001; Manly and Sanderson 2002; Gotelli and Entsminger 2003), I decided to use both the swap algorithm and the modified "Knight algorithm" incorporated into EcoSim and compare results obtained from each one.

Abundance-Weighted Simulation 1 (ABW1): Species abundance weighted rows-Fixed columns. In this simulation the observed number of species at each site is maintained as in the original data set, but species occurrences at each site are determined by their landscape relative abundance. I calculated a weighting factor by counting the number of captured individuals for each species for all sites and then correcting by the number of trapnights used at the vegetation type(s) where each species was captured since trapping effort at each site was different. This density per unit of effort was then multiplied by total trapnights for all the study to obtain an estimate of relative density of each species over all sites that I expressed in a percentage basis (Figure 4). I entered this percentage of relative abundance for each species into EcoSim as an independent weight for this simulation. However, I was only able to do this simulation with my dataset and with the restricted set of Vargas-Contreras and Hernandez-Huerta (2001), since I did not sample all vegetation

types reported in the full dataset of these authors and thus had no abundance data for species on those sites.

Abundance-Weighted Simulation 2 (ABW2): Species abundance weighted rows-Equiprobable columns. Just as in the previous simulation species occurrence is determined by an abundance weighting, but in this case each site is equally likely to be represented since they are treated as homogeneous entities.

Since the last three simulations (SIM2, ABW1 and ABW2) have the potential to create degenerate matrices, in which either rows or columns are empty, I either retained, discarded or fixed them as further options in each simulation. When retained, all simulated matrices were used to generate the frequency distribution of null communities. Conversely, when discarded only non-degenerate matrices were used to generate this frequency distribution. Finally, degenerate matrices were "fixed" by randomly transferring one of the cell occurrences from an occupied row or column to an empty row or column.

RESULTS

Trapping results.—During trapping for this study, I captured 789 individuals, in 1,365 capture events, which represent 14 rodent species. The TSDF had the highest number of species (10) with the rest of the vegetation types (CPV, TS, CF) having 5 species each (Appendix II). At the TSDF I also detected two introduced species (*Mus musculus*, *Rattus* sp.) but I did not included them in the analyses. Turnover of species

was almost complete between the lowest elevation sites (CPV) to the sites at highest elevation (CF), with only one species, *Oligoryzomys fulvescens*, shared between all vegetation types. In general, *Peromyscus* species dominated each one of the communities I sampled and therefore were the most abundant species at the landscape level. On the other end of the abundance distribution, *Reithrodontomys* species were quite rare and were only represented by a few individuals over all sites (Figure 4). Tail clip samples of *Peromyscus* individuals that were not readily identifiable in the field provided enough material to sequence the mitochondrial cytochrome *b* gene. A neighbor-joining dendrogram was constructed from Tamura-Nei distances between haplotypes (Saitou and Nei 1987; Tamura and Nei 1993). Species identification was assessed from placement of lineages within monophyletic clusters of published *P. pectoralis* and *P. levipes* cytochrome *b* sequences. In all cases, sequences of each individual that I tested grouped unequivocally with either one of the reference samples. These genetic identifications confirmed their specific status and consequently provided an accurate evidence for the presence of each species at the communities I sampled.

Species accumulation functions.—All vegetation types had adequate samples and in all cases the number of observed species and the value of the asymptote predicted by the best fitting model were the same (Figures 5, 6, 7, 8). The data for each vegetation type was fitted to each of the three models in Appendix I, being in all cases the exponential function the best-fitting model (Table 1). The SAF application calculates a likelihood ratio that provides a plausibility scale to assess the three models (Diaz-Frances and Soberon 2005). In all vegetation types, except for the CF, there is

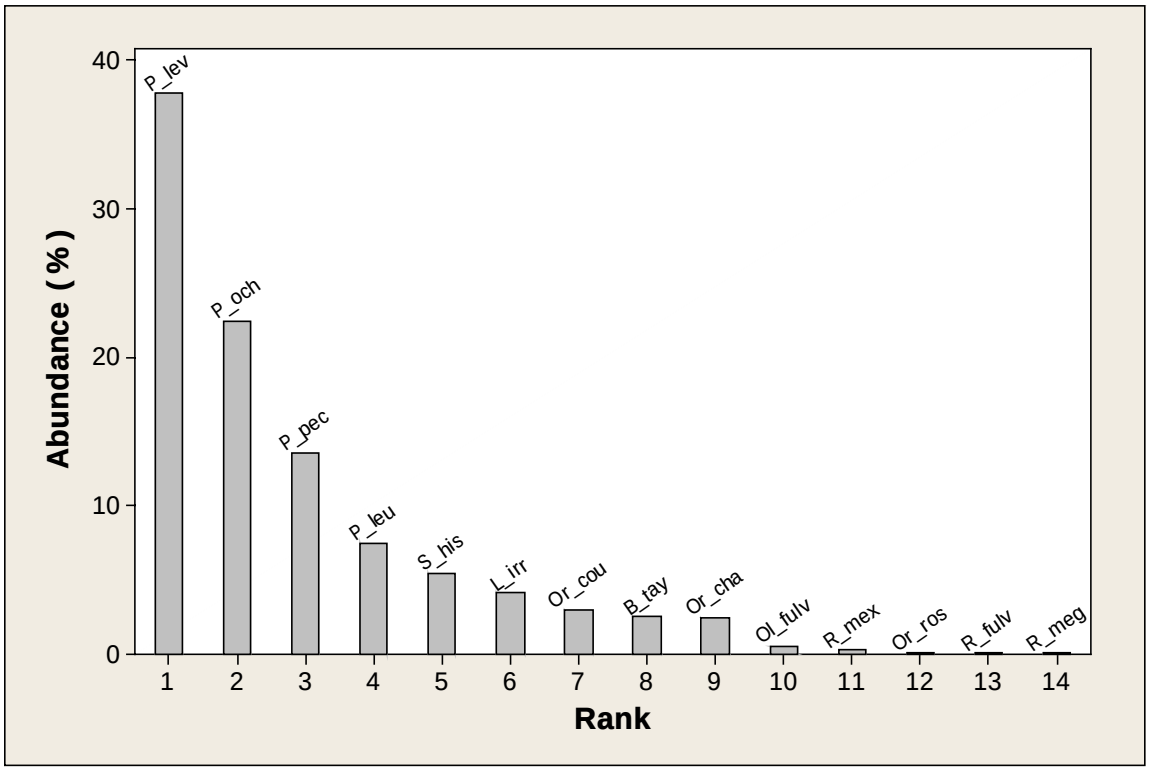

Figure 4.—Rank abundance pattern for the 14 rodent species present at the sampled vegetation types from the eastern slopes of El Cielo Biosphere Reserve. Species abbreviations as in Appendix II.

very strong evidence that the exponential function is the most adequate model. For example, for the CPV, the exponential model is 109,745 times more probable than the Clench model and 1,987,816 times more probable than the logarithmic model. For the CF, the evidence in favor of the exponential model is not as strong, but even if the Clench model is selected, the asymptote of this model only reaches six species. Overall, there is strong evidence that each site was adequately sampled and that the list of species

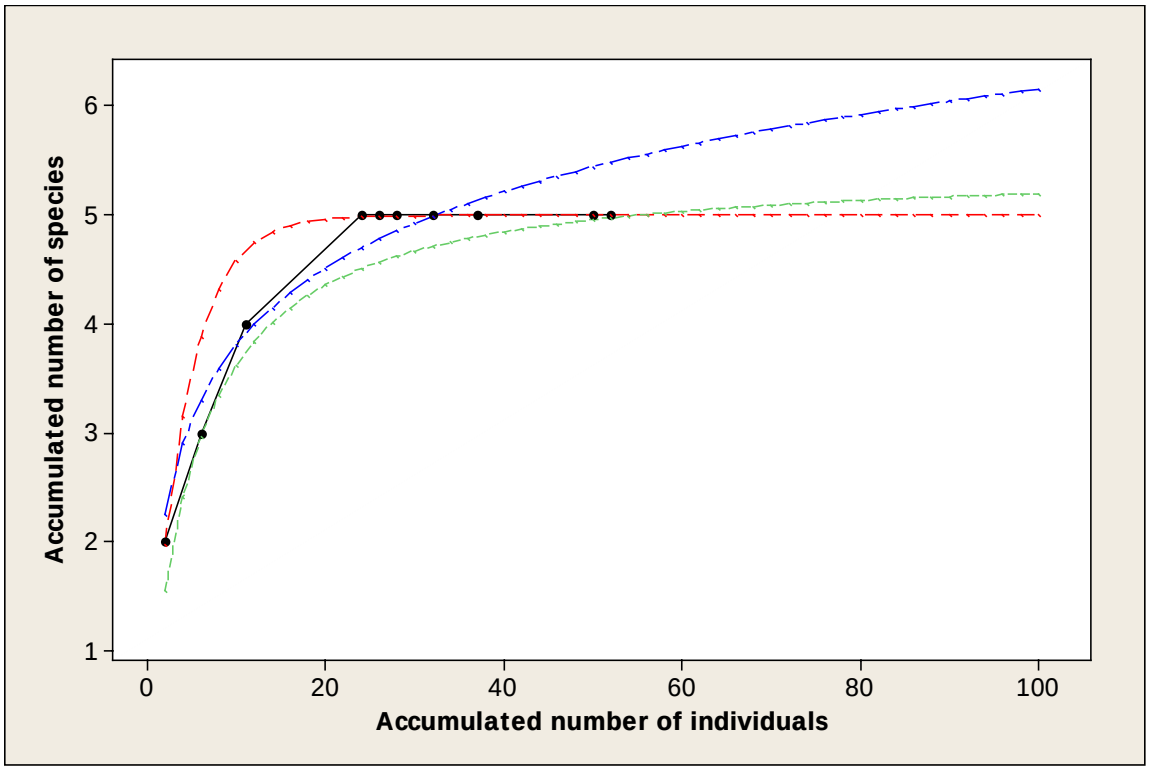

Figure 5.—Fit of three models of species accumulation functions for the CPV sites dataset. Black line and circles represent observed accumulated species number; blue line the fit to the logarithmic model; Red line the fit to the exponential model and green line the fit to the Clench model. See text for model fitting details.

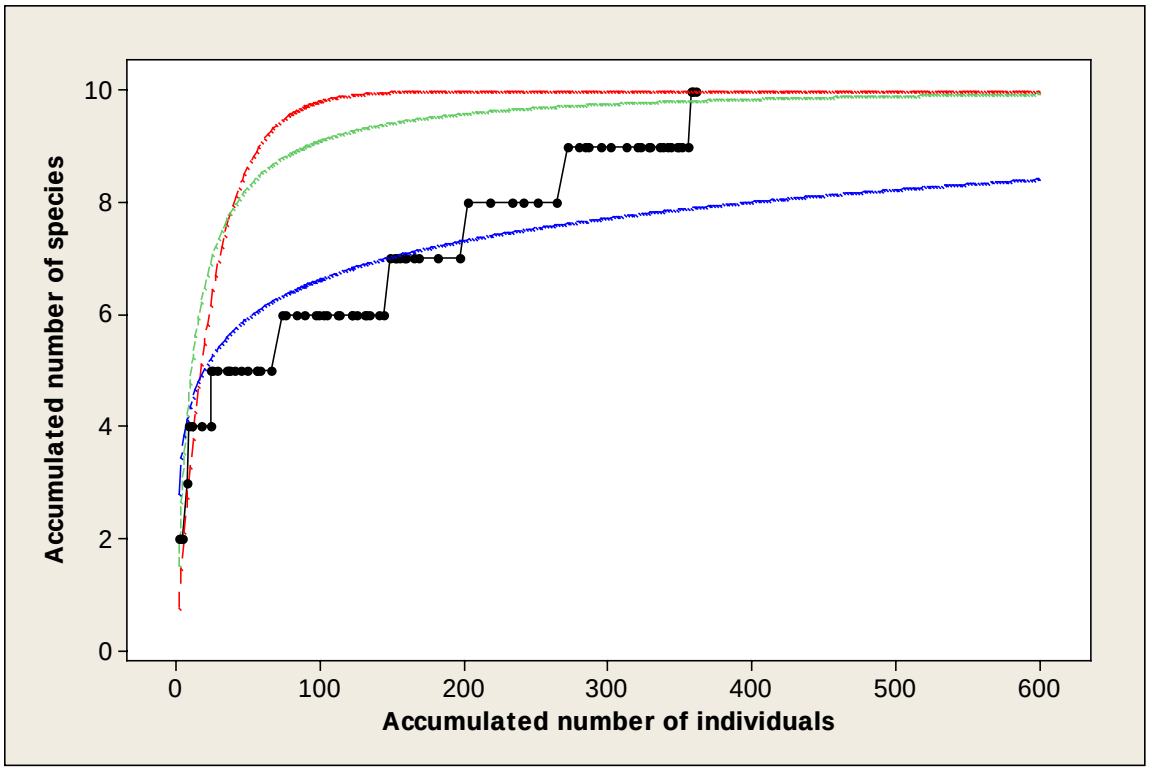

Figure 6.—Fit of three models of species accumulation functions for the TSDF sites dataset. Black line and circles represent observed accumulated species number; blue line the fit to the logarithmic model; Red line the fit to the exponential model and green line the fit to the Clench model. See text for model fitting details.

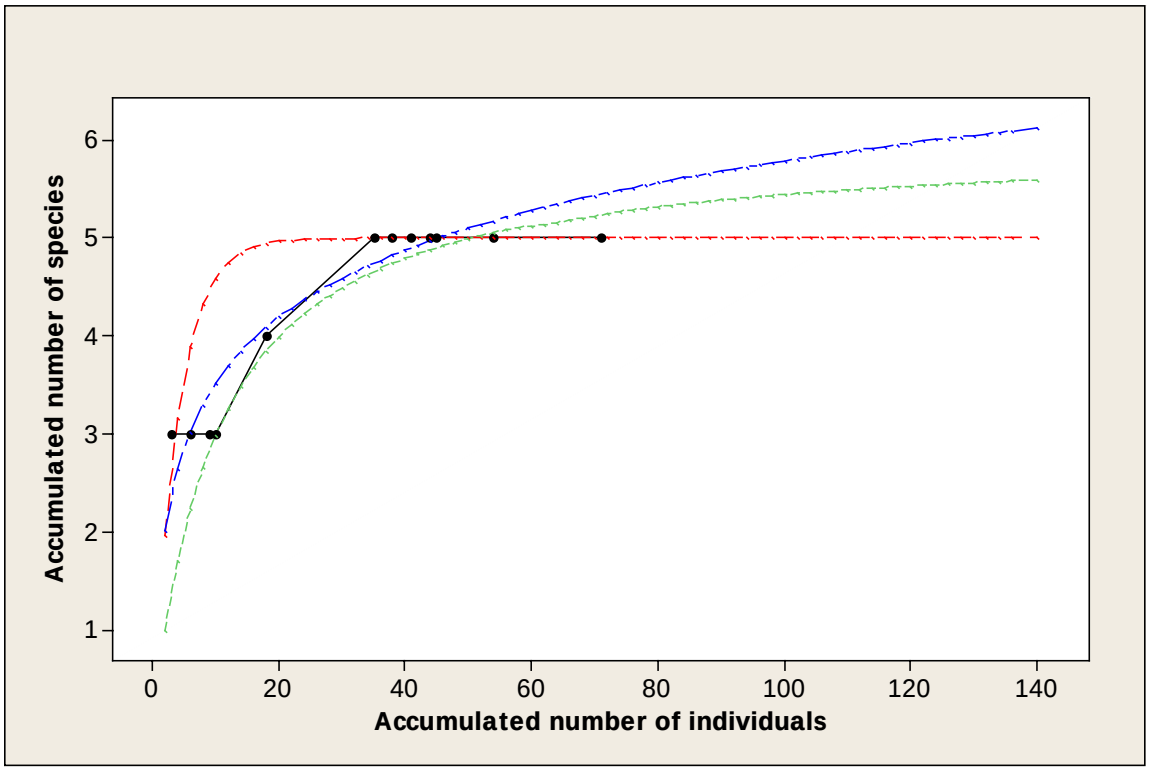

Figure 7.—Fit of three models of species accumulation functions for the TS sites dataset. Black line and circles represent observed accumulated species number; blue line the fit to the logarithmic model; Red line the fit to the exponential model and green line the fit to the Clench model. See text for model fitting details.

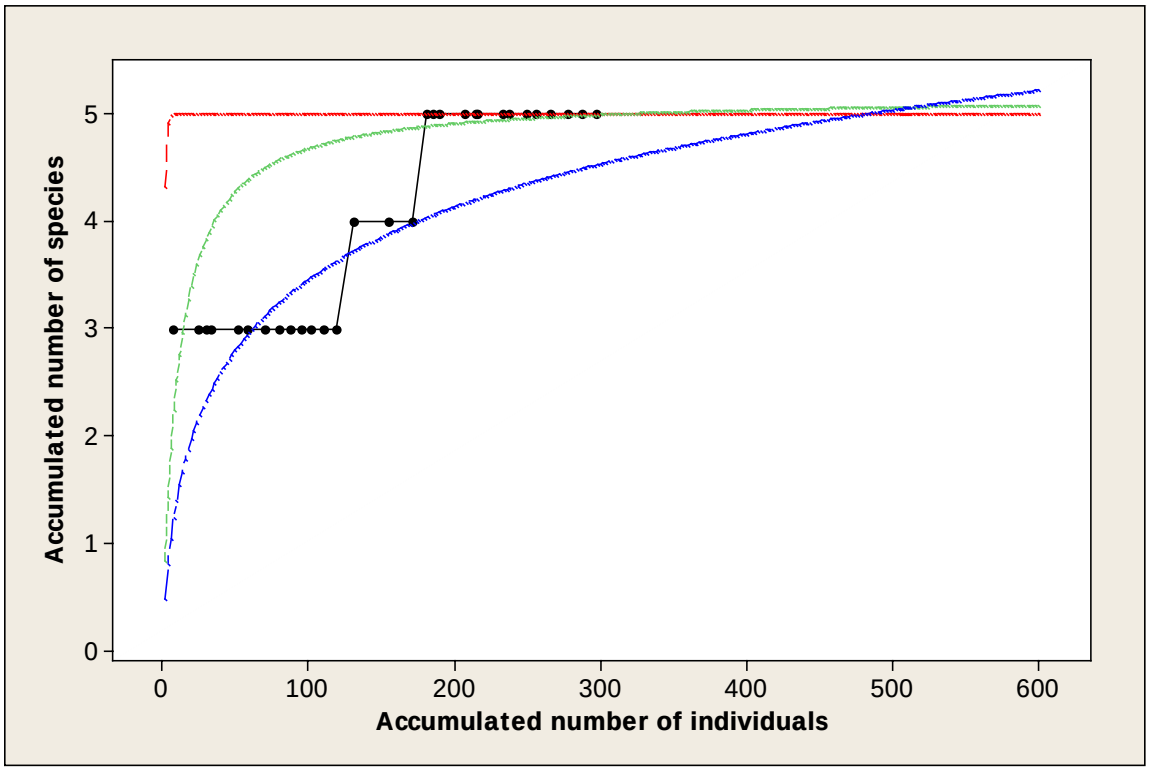

Figure 8.—Fit of three models of species accumulation functions for the CF sites dataset. Black line and circles represent observed accumulated species number; blue line the fit to the logarithmic model; Red line the fit to the exponential model and green line the fit to the Clench model. See text for model fitting details.

Table 1.—Estimated parameters for the species accumulation models for each one of the vegetation types sampled. Abreviations are: *a* and *b* are fitted parameters; TNS, estimated total number of species; LR, likelihood ratio. 1/LR indicates how many times more plausible each model is from the ones below it in this table. The Logarithmic model is unbounded and the other two reach asymptotes that correspond to TNS.

Vegetation type	Model	a	b	TNS	LR	1/LR
CPV	Exponential	1.250	0.250	5	1	1
	Clench	1.076	0.197	6	0.000009	109,745
	Logarithmic	4.094	3.597	n/a	0.000001	1,987,816
TSDF	Exponential	0.397	0.040	10	1	1
	Clench	0.898	0.089	11	<0.000000001	>1,000,000,000
	Logarithmic	7.549	21.990	n/a	<0.000000001	>1,000,000,000
TS	Exponential	1.250	0.250	5	1	1
	Logarithmic	3.254	15.766	n/a	0.00000046	2,166,580
	Clench	0.594	0.099	7	0.00000025	3,910,580
CF	Exponential	5.025	1.005	5	1	1
	Clench	0.494	0.096	6	0.306796	3.26
	Logarithmic	0.307	10.906	n/a	0.064787	15.44

generated for each rodent community is not biased by under-sampling and thus can be used to make comparative analyses between sites.

Null model analyses.—I obtained consistent results between both indices I used, C-score and CHECK. For any given simulation the CHECK index yielded higher probabilities that the observed index was equal or larger than the mean index from the simulations. This was an expected outcome given that the CHECK index is stricter in its detection of randomness given that is based comparison of number of perfect

checkerboard species pairs instead of an average "checkerboardnesss" measured by the C-score (Gotelli 2000). However, I found contrasting results of all null model analyses between the three datasets I analyzed. For all null model simulations with both indices both the full dataset and the restricted dataset of Vargas-Contreras and Hernandez-Huerta (2001) failed to show significant differences, at the 0.05 level, except for a single case (Tables 2 and 3). Instead, significant results for my fieldwork dataset depended greatly on model assumptions of each simulation.

For SIM9, both indices and algorithms that I tested provided significant results that point towards a non-random structure of species co-occurrences between the vegetation types I sampled (Tables 2 and 3). But if the strict constraints of SIM9 are relaxed and sites are considered equiprobable (SIM2), then analyses with both indices yielded non-significant results. Non-significant results in this simulation were independent of how degenerate matrices were treated. Due to the nature of the model, very few or no degenerate matrices were created during the creation of simulated communities. For the other two simulations, ABW1 and ABW2, results were strongly dependent on how degenerate matrices were treated. In all four cases, when the degenerate matrices were retained and used to generate the mean index value for the simulated communities, I obtained highly significant results (Table 2 and 3). There were too few non-degenerate matrices to perform analyses using this type exclusively. Finally, for these same simulations, if degenerate matrices are fixed, then non-significant results were obtained in all four cases.

DISCUSSION

My fieldwork-based study of rodent species distributions among vegetation types on the eastern slopes of ECBR uncovered a non-random pattern of species co-occurrences along this elevational gradient. Null model analyses of two versions of an independently derived dataset of species distributions over this same gradient failed to detect any differences from a random pattern. The final species list from my fieldwork surveys had substantial differences with the species listed for each vegetation type in Vargas-Contreras and Hernandez-Huerta (2001). Contrasting results between these two datasets are due to the way species lists were generated. Differences in survey efforts and species identification methods have a profound effect in the final results of null model analyses of these species distributions records. Just as comparisons of species richness between sites are affected by differences in survey completeness (Colwell and Coddington 1994; Moreno and Halffter 2000), null model analyses of species co-occurrences will be severely biased by incomplete species lists (Gotelli and Graves 1996). I present evidence that adequate sampling generated the species records from each vegetation type, whereas Vargas-Contreras and Hernandez-Huerta (2001) failed to present any evidence for survey completeness. Differences between trapping effort between these two studies are also striking. These authors reported a total trapping effort of 1,300 trap-hours. Considering that each night trapping period as consisting of 12 hours then the total effort for my study, in an equivalent notation, consisted of 236,544 trap-hours. Vargas-Contreras and Hernández-Huerta (2001) complemented

Table 2.—Simulation results for the three datasets tested using the C-score index. P value corresponds to the probability that the observed index is equal or greater than the expected mean from the simulations. A significantly larger observed C-score means a non-random structure of species co-occurrences. Abbreviations are: SSA, Sequential Swap algorithm; RKTA, Random Knight Tour algorithm; DMR, degenerate matrices Retained; DMD, degenerate matrices discarded; DMF, degenerate matrices fixed; VC-HH, Vargas-Contreras and Hernandez-Huerta; and np, simulation not possible.

		Present study dataset		VC-HH full dataset		VC-HH full dataset	
Observed mean		0.945		0.6081		0.43956	
Simulation		Expected index mean	P-value	Expected index mean	P-value	Expected index mean	P-value
SIM9							
	SSA	0.78175	0.002	0.582	0.13	0.44434	0.57
	RKTA	0.7731	0.001	0.608	0.14	0.44046	0.51
SIM2							
	DMR	0.85541	0.17	0.826	0.98	0.89256	0.99
	DMD	0.85268	0.17	0.826636	0.98	0.899305	0.99
	DMF	0.85433	0.17	0.82924	0.98	0.89234	0.99
ABW1							
	DMR	0.24733	>0.0001	n/a	n/a	0.0817	>0.001
	DMD	np	np	n/a	n/a	np	np
	DMF	0.80744	0.15	n/a	n/a	0.27549	0.15
ABW2							
	DMR	0.38004	>0.0001	n/a	n/a	0.25005	0.08
	DMD	np	np	n/a	n/a	np	np
	DMF	0.93148	0.5	n/a	n/a	0.777	0.98

Table 3.—Simulation results for the three datasets tested using the number of checkeboard species as an index. P value corresponds to the probability that the observed index is equal or greater than the expected mean from the simulations. A significantly larger observed number of checkerboard species pairs means a non-random structure of species co-occurrences. Abreviations as in Table 2.

		Present study dataset		VC-HH full dataset		VC-HH full dataset	
Observed mean		33		44		6	
Simulation		Expected index mean	P-value	Expected index mean	P-value	Expected index mean	P-value
SIM9							
	SSA	29.4	0.03	43.585	0.44	5.906	0.62
	RKTA	29.8	0.05	45.295	0.62	6.3446	0.71
SIM2							
	DMR	33.3	0.66	55.58	0.97	18.53	0.99
	DMD	33.23	0.66	55.52	0.97	18.54	0.99
	DMF	33.24	0.66	55.47	0.97	18.53	0.99
ABW1							
	DMR	1.65	>0.001	n/a	n/a	0.315	0.06
	DMD	np	np	n/a	n/a	np	np
	DMF	27.24	0.15	n/a	n/a	6.69	0.61
ABW2							
	DMR	4.55	>0.001	n/a	n/a	2.901	0.17
	DMD	np	np	n/a	n/a	np	np
	DMF	34.4	0.73	n/a	n/a	23.1	0.99

their fieldwork with published records of species presences and museum specimens, but even there I found mistakes in the use of that information. For example, these authors list *Peromyscus levipes* as present in the TSDF based on a previous work (Alvarez 1963) but a careful review of this publication failed to confirm presence of this species at that vegetation type. Lastly, a relevant component unique to my survey methods was the genetic identifications of individuals of *P. levipes* and *P. pectoralis.* This identification method was a completely unambiguous process that provided an accurate way of documenting each species presence among the vegetation types that I sampled. These two species are easily confused because of their similar external characteristics (Hooper 1952; Schmidly 1972; Schmidly and Hendricks 1984), and since Vargas-Contreras and Hernández-Huerta (2001) do not specifically mention the species identification methods they used, there is a good possibility that some individuals were misidentified. Given this accumulation of differences, it is then not surprising the contrasting null model analyses results between them. Given the list of inadequacies I have found in Vargas-Contreras and Hernández-Huerta (2001) dataset to carry out a proper null model analysis, I can only derive conclusions from analyses of my own fieldwork dataset.

Null model analyses results for my dataset differed depending on model assumptions for each of the simulations, but, as stated above, I found no differences between results for both indices I used. All four models address community composition objectively, yet the variations in the model assumptions result in markedly different interpretations against the pattern observed in the real assemblages. Results for SIM9 were significant, independently of what randomization algorithm was used

(Sequential Swap algorithm or Random Knight Tour algorithm). Since this simulation maintains both row and column totals, richness differences between sites and species differences in number of sites they occupy are maintained. This simulation had the most restricted "null space" of all the simulations I tested, ie., it produced a limited number of null communities as compared to the other simulations. Careful selection of the appropriate null space is critical to derive conclusion and to compare results obtained from different models (Sanderson 2004). As the null space is augmented the probability of incorrectly rejecting the null hypothesis (Type I error) grows larger since the model becomes "too null" and thus will very likely encompass the real community (Gotelli and Graves 1996). On the other hand, if the model is too restricted then the probability of falsely accepting the null hypothesis (Type II error) becomes larger since because the simulations so closely reflect the observed data that the null hypothesis can never be rejected (Gotelli and Graves 1996). A systematic analysis of Type I and Type II errors showed that SIM9 used in conjunction with the C-score had good properties against both type of errors and also was able to detect non-random pattern even in datasets that had "random noise" imbedded in the co-occurrence patterns (Gotelli 2000). So, under the assumptions of this model my data showed that species co-occurrences are being driven from some mechanistic process and not random processes alone.

However, opposite to results from SIM9, the outcome for SIM2 points towards a random structure. Under the assumptions of SIM2 results were non-significant independently of how degenerate matrices were handled. SIM2 corresponds to a simple model of independent species colonization where each site is equiprobably selected.

Observed differences in species richness of sites are thus eliminated in the null assemblages. For this model very few or no degenerate matrices existed in the null communities as evidenced by the lack of differences between results for each way these matrices were handled. Simulations ABW1 and ABW2 had basically the same outcomes that were highly dependent on how degenerate matrices were considered. When degenerate matrices were retained the results were highly significant, but when these degenerate matrices were "fixed" by randomly adding a species presence to correct any empty row or column then results were highly non-significant. The reason for these extremes is a reflection of the species relative abundance pattern at the landscape level (See figure 4). When species incidences in the null communities are weighted by their landscape relative abundances two main trends are created: (1) abundant species will tend to co-occur together since they will likely occupy most of the vegetation types and (2), rare species may not even appear in the null communities. This last trend is made evident when all analyses that discarded degenerate matrices were impossible to perform since they were too many rows (species) with zero sums (See Tables 2 and 3). Fixing these matrices by randomly adding a species presence ends up with null communities that have almost the same co-occurrence pattern for rare species as the real community.

Overall, I only obtained consistent significant results for SIM9 with the rest of simulations being inconsistent in their outcomes. SIM9 has been proven to be an adequate simulation to detect non-randomness in species co-occurrences (Gotelli 2000), and has been relied as the single proof to test some patterns (Gotelli and McCabe 2002) but exploration of other models is not a futile exercise. Relying on a single simulation

model cancels one of the great advantages of null model analyses that consist on the insights that variations in model assumptions can provide. In my study simulations ABW1 and ABW2 made evident a feature of my dataset: large differences between abundant and rare species are having a strong impact on the results of the analyses. Since most rare species were in the genus *Reithrodontomys* and the most abundant species in the genus *Peromyscus,* analyses that included all rodent species might be affected by the so called "dilution effect". Analyzing entire assemblages can mask actual non-random patterns between some species if these are imbedded in an otherwise non-interacting species group. To uncover that pattern, species need to be separated into objective groupings. It has been shown that designation of species into ecological or taxonomic guilds clearly affects the outcome of null model tests (Vuilleumier and Simberloff 1980; Graves and Gotelli 1993).

Given the outcome from my initial analyses, I decide to do a post-hoc test of species distributions from my dataset but now assigning species to objective guilds. Delineating guilds is not a trivial task (Simberloff and Dayan 1991) and should be established by criteria independent of the co-occurrence data that is being tested (Connor and Simberloff 1983). Since quantitative and detailed information of food use in these rodent species at these sites is lacking, I used taxonomic and body mass criteria to group species. Analyses within taxonomic guilds were restricted to *Peromyscus*, *Oryzomys* and *Reithrodontomys* genera because only these had three or more species. I delineated body mass guilds based on major differences between species. I first ordered species from smallest to largest, and then calculated species ratios between adjoining species.

These ratios were almost uniform except for two major breaks used to divide species into three groups: small, medium and large. Body mass averages per species and guild designations are in Appendix II.

After I designated species into these guilds, I ran the same simulations, as with the full dataset, to confirm that indeed there were substantial differences between results for each of the created guilds (Tables 4 and 5). Within the taxonomic guilds I obtained a clear trend: *Peromyscus* species had significant results under almost all model assumptions, whereas in the genus *Oryzomys* the contrary was true. The *Reithrodontomys* species guild could not be analyzed because observed values for the indices in this group were zero such that any index value from the simulations will accept the null hypothesis of random species co-occurrences. Care should be taken when interpreting results for these groups, because they represent very few species. No systematic study to assess the effects of matrix size on null model results has been published. However, if small numbers of species are used in the analyses, there is a limited amount of variability that can be incorporated into the randomizations, which may inflate type II error (K. Winemiller, personal communication).

Results from the body mass guilds are more remarkable and do not suffer from the possible effects of extreme small sizes. I could only test two guilds, ie., small and medium rodents, since the third guild comprised a single species. These two guilds are quite contrasting in different aspects: the small rodent group consisted of 5 species with an average body mass of 9.8 g and represented only 3.57% of the individuals at the

Table 4.—Simulation results for species co-occurrences within two taxonomic guilds using C-score and number of checkerboard species pairs (CHECKER) as measuring indices. Species distributions were taken from the fieldwork surveys of the present study. P value corresponds to the probability that the observed index is equal or greater than the expected mean from the simulations. A significantly larger observed index means a non-random structure of species co-occurrences. Abreviations as in Table 2.

		Peromyscus (4 spp)				*Oryzomys* (3 spp)			
		CHECKER		C-Score		CHECKER		C-Score	
Observed index		5		1.5		2		1.33	
Simulation		Expected index mean	P-value	Expected index mean	P-value	Expected index mean	P-value	Expected index mean	P-value
SIM9									
	SSA	4.0601	0.06	1.4258	0.55	2.00	1.00	1.08	0.24
	RKTA	4.0783	0.08	1.41298	0.48	2.00	1.00	1.05	0.15
SIM2									
	DMR	2.9306	0.02	1.01952	0.20	1.76	0.75	0.925	0.26
	DMD	3.7748	0.04	1.34008	0.39	3.00	1.00	1.687	0.26
	DMF	3.8313	0.02	1.25237	0.29	3.00	1.00	1.667	1.00
ABW1									
	DMR	1.8641	0.01	1.2125	0.37	0.102	0.05	0.52977	0.01
	DMD	4.0455	0.05	1.2969	0.32	np	np	np	np
	DMF	4.0634	0.06	1.3496	0.38	3	1.00	1.66667	1.00
ABW2									
	DMR	1.4269	0.01	0.8366	0.18	0.269	0.03	1.01483	0.20
	DMD	3.7682	0.02	1.2174	0.24	3	1.00	1.66667	1.00
	DMF	3.8654	0.04	1.3172	0.37	3	1.00	1.66667	1.00

Table 5.—Simulation results for species co-occurrences within body mass guilds using C-score and number of checkerboard species pairs (CHECKER) as measuring indices. Species distributions were taken from the fieldwork surveys of the present study. P value corresponds to the probability that the observed index is equal or greater than the expected mean from the simulations. A significantly larger observed index means a non-random structure of species co-occurrences. Abreviations as in Table 2.

		Small rodents (5 spp)				Medium rodents (8 spp)			
		CHECKER		C-Score		CHECKER		C-Score	
Observed index		0		0.2		18		1.39	
Simulation		Expected index mean	P-value	Expected index mean	P-value	Expected index mean	P-value	Expected index mean	P-value
SIM9									
	SSA	np	np	0.2	1.00	15.700	0.030	1.188	0.002
	RKTA	np	np	0.2	1.00	15.730	0.030	1.183	0.002
SIM2									
	DMR	np	np	0.532	0.87	13.490	0.007	1.016	0.001
	DMD	np	np	0.5286	0.88	13.825	0.008	1.047	0.001
	DMF	np	np	0.52677	0.87	14.268	0.002	0.664	>0.001
ABW1									
	DMR	np	np	0.21021	0.81	3.44	0.0001	0.7397	0.02
	DMD	np	np	0.21404	0.82	np	np	np	np
	DMF	np	np	0.21124	0.81	14.91	0.030	1.05239	0.003
ABW2									
	DMR	np	np	0.34635	0.60	2.9	>0.0001	0.60292	0.01
	DMD	np	np	0.49765	0.91	np	np	np	np
	DMF	np	np	0.67025	0.94	14.24	0.020	0.99236	0.001

landscape level. On the contrary, the medium rodent guild had 8 species of an average body mass of 29.6 g, which accounted for 91% of the individuals for all sites. Because of lack of checkerboard species pairs (observed index value of zero) null model tests for small rodents were either non-significant or not possible. For medium rodents I obtained highly significant results under all model assumptions. It is clear from tests for these two guilds that rare species co-occur at random over the vegetation types I tested, whereas abundant species do not follow a random pattern.

Addition of independent weights for species and sites to null model analysis of species co-occurrences is still a relatively unexplored area within ecology (Gotelli 2000). Most of the time researchers have only used species presence-absence data to carry out null model analyses. Additional information like species abundances has been only rarely incorporated into co-occurrence analyses, although it has been shown that they can be highly relevant to test presumed patterns (Gotelli et al. 1987; Graves and Gotelli 1993). My study confirms that inclusion of additional information into simulations models has the capability of providing further insights than if a single null model simulation is used to test for a co-occurrence pattern. A challenge for integrating ancillary information, eg. species abundances, dispersion abilities and site differences, to null model analyses is the difficulty to obtain this information, but this should not be a reason to abandon the inclusion of these additional tests.

For advocates of the competition paradigm the lack of pattern between rare species and the strong pattern for abundant species that I found could be interpreted as evidence for a competition driven exclusion mechanism that is driving these

assemblages (Grant 1972; Diamond 1975; Grant and Schluter 1984; Fox and Brown 1993; Kelt, Taper, and Meserve 1995; Brown et al. 2002). However, a mechanistic explanation cannot be reached solely by these analyses, because it goes beyond what these null models can portray, although they are unmistakably test existence of patterns.

Two different, and non-mutually exclusive, alternative hypothesis need to be considered also as possible explanations of this pattern. The first is that the pattern may be a reflection of habitat checkerboards, ie., species are associated with different abiotic features of the sites which leads to less co-occurrence than expected by chance (Lomolino 1999) . The second is that historical and phylogenetic processes may have led to less coexistence than expected by chance (Brooks and McLennan 1993; Losos 1996). Even more complexity is added by the fact that all three hypothesis are not mutually exclusive and can be linked, ie., competition may have driven species evolution to occupy separate microhabitats (Morris 1999).

Current knowledge of some of these species gives some insight on this issue. As shown in my study *Peromyscus* species are within the guild of species that co-occur less often than expected by chance and have a large part in creating this pattern. Elevational distribution of *Peromyscus* species at ECBR follow the same pattern as in the rest of Tamaulipas, Texas and New Mexico with *P. leucopus* occurring commonly up to 360 meters, *P. pectoralis* using intermediate zones and *P. levipes* higher elevations (Alvarez 1963; Schmidly and Hendricks 1984; Geluso 2004). In the San Carlos Mountains of Tamaulipas *P. pectoralis* and *P. levipes* had complementary density patterns that differed between the habitats where they occurred (Schmidly and Hendricks 1984) but

their separation was not as complete as in the results from my study. The differential abundance pattern is repeated along the elevational range of the Davis Mountains of western Texas with *P. pectoralis* being more abundant at lower elevations and another *Peromyscus* species, *P. boylii*, being dominant at higher elevations (Schmidly, 1977). Recent molecular phylogenetic studies have found that *P. boylii* is highly related to *P. levipes,* and although their exact relationship to *P. pectoralis* is unclear, they are at best a distant lineage to this latter species (Tiemann-Boege et al 2000). Throughout its range *P. pectoralis* occurs only at intermediate elevations even if rocky habitats are present at other zones (Geluso 2004). Studies in Texas and New Mexico have shown that at higher elevations this kind of habitat is dominated by *P. boylii*, *P. nasutus* and *P. truei,* with low elevations dominated by *P. eremicus* (Schmidly 1977; Cornely et al 1981; Dalquest and Stangl 1986; Geluso and Geluso 2004). This pattern is repeated in Tamaulipas at the San Carlos Mountains (Schmidly and Hendricks 1984) and confirmed by my study, albeit separations were with other species: *P. leucopus* at lowlands and *P. levipes* and *P. ochraventer* at higher zones. Also, at ECBR species separations between the sites I sampled were total, in contrast with only shifting abundance patterns at other sites. Whatever is driving the tendency of these species to segregate it is acting stronger at ECBR. The distribution of *Peromyscus* species over elevational gradients from these mountains over eastern Mexico and south-central USA is highly consistent in pattern suggesting a more general explanation, perhaps with a strong phylogenetic component. Available phylogenetic data (Tiemann-Boege et al 2000), although partial, allows the observation that at each mountain gradient each zone is occupied by a species of a

different lineage within the genus *Peromsycus*. A complete phylogeny of all *Peromsycus* species occurring at this region is needed to assess the generality of this observation and the role of species evolutionary histories in the structure of these communities.

Detailed studies of species, shown to be non-randomly segregated, will be needed to identify specific mechanisms by which these communities are organized and maintained. Careful comparative designs such as the one used to assess distribution of Andean birds over an elevational gradient (Terborgh and Weske 1975) and an explicit incorporation of phylogenetic information in community structure studies (Winemiller 1991; Losos 1996) have great potential to augment our understanding of these systems.

CHAPTER III

RELEVANCE OF TEMPORAL NICHE DYNAMICS FOR TWO RODENT COMMUNITIES AT EL CIELO RESERVE

Ecological niches have a multidimensional nature, but it has been suggested that the three principal dimensions are space, food and time (Schoener 1974). Resource partitioning studies have attempted to determine underlying mechanisms of community structure by quantifying niche dimensions and overlap of component species (Grant 1972; Pianka 1973). The majority of studies addressing species coexistence in small mammals has been either directed at habitat selection (Morris 1987; Rosenzweig 1987) or food type partitioning (Dayan and Simberloff 1994), but temporal partitioning has seldom been explored and it has even been considered uncommon (Schoener 1986). However, evidence of niche partitioning in the time axis has accumulated, and has been demonstrated for both vertebrate and insect communities on both seasonal and diel scales (O'Farrell 1974; Tokeshi 1986; Ziv et al. 1993; Lockwood et al. 1996; Jepsen et al. 1997; Albrecht and Gotelli 2001; Arrington and Winemiller 2003). Partitioning at larger temporal scales, ie. seasonal or annual, can generally be explained by correlated differences in resource dynamics (Loreau 1989) whereas differences at smaller scales, ie. diel cycles, are more likely to involve an interpretation of interference competition (Carothers and Jaksic 1984). Further possible explanations may exist with the added interplay of predation and historical, ie. phylogentic, factors influencing foraging behaviors, which form the main component of activity patterns (Kotler et al. 1991; Fraser et al. 2004; Kronfeld-Schor et al. 2001). Research on the ecological significance

of temporal niche patterns has the potential to elucidate mechanisms of community assembly.

Extensive research in chronobiology has shown that time assessment mechanisms present in many organisms are complicated and sophisticated internal devices. Advances in the last decade on the nature of circadian rhythms at the physiological, biochemical and molecular levels are considered major breakthroughs that have transformed our ideas about nature (Kronfeld-Schor and Dayan 2003). However, most chronobiologists have failed to frame their discoveries with regard to the interplay of animals and their environments, and most ecologists have disregarded research on the relevance of temporal niche patterns and their possible ecological effects (Marques and Waterhouse 2004; Morgan 2004). The ecological significance of diel rhythms in community assembly and coexistence of species remains largely unknown (Kronfeld-Schor and Dayan 2003). It has been shown that temporal activity pattern strategies do have an impact on individual fitness (DeCoursey 2004), and as such are subject to selection forces. Clearly, research of the interface between species interactions and activity patterns offers great potential to gain evolutionary insight on the role of time as a niche axis.

Even though small mammals have been used to address many theoretical ecology issues, their activity patterns have not been as extensively researched (Halle and Stenseth 2000). Most studies have been restricted to simple reports of activity patterns (Blanchong and Smale 2000; Eccard et al. 2004) and comparisons between species pairs (Drickamer 1987; Ryan et al. 1993; Bruseo and Barry 1995) with only a few addressing

species patterns in whole communities (Kenagy 1973; O'Farrell 1974; Vieira and Baumgarten 1995) and none using a null model approach to address temporal overlap patterns. From this last group, only one study was done with a tropical community.

In the present study, I report the first use of a null model to statistically test the community wide patterns of temporal niche overlap for small mammals, rather than species pairs only, as in previous studies. I used capture frequencies in 2-hr nighttime intervals to document species activity patterns during three summer seasons at a subtropical site in northeastern Mexico. I compared observed patterns to those expected under the null hypothesis of independent activity patterns for each species.

MATERIALS AND METHODS

Study area.—I conducted my study as part of a larger project about rodent community dynamics at El Cielo Biosphere Reserve (ECBR). This reserve encompasses approximately 144,500 ha in southwestern Tamaulipas, Mexico. A sharp altitudinal gradient is present in the eastern part of the Reserve, with a pronounced change in elevation of 200 to 1,800 meters. Three different vegetation zones occur over this gradient: Tropical Subdeciduous Forest (TSDF), Cloud Forest (CF) and Pine-Oak Forest (POF). I conducted my fieldwork in the southeast portion of the Reserve within the limits of Gomez Farias municipality (23 03’42” N and 99 12’18” W). I established two sampling sites located one in TSDF and one in CF. At the TSDF site the dominant tree species are *Bursera simaruba*, *Brosium alicastrum*, *Lysiloma divaricata*, *Mirandaceltis monoica*, *Croton niveus*, *Savia sessiliflora*, *Drypetes lateliflora*, *Acalypha schiedeana*,

and *Ficus* spp. (Sosa 1987; Valiente-Banuet et al. 1995). The understory of this forest has *Acalypha schiedeana*, *Urera caracasana*, *Chamedorea radicalis* and *Syngonium podophyllum* as prevailing species (Valiente-Banuet et al. 1995). Within this vegetation type there are open areas, both natural and man-made, where common plants are *Mirabilis jalapa*, *Jacobinia incana*, *Gibasis pellucida*, *Paspalum paniculatum*, *Cenchrus echinatus*, *Argemone mexicana*, *Sclerocarpus uniserialis* and *Canna indica* among others (Mora et al. 1997). Elevation at this site was 320 m with a mean annual temperature of 22.8 ºC and a total annual precipitation of 1,852 mm (Puig and Bracho 1987). In contrast, the CF site was at 1,320 m where dominant canopy species are *Liquidambar styraciflua*, *Quercus sartorii*, *Q. germana*, *Clethra pringlei*, *Magnolia shciedeana*, *Podocarpus reichei*, *Acer skutchii*, *Carya ovata* and *Cercis canadensis* (Puig et al. 1987a). In this forest, the lower strata are codominated by *Ternstroemia sylvatica*, *Meliosma oaxacana* and *Eugenia capuli*, with common presence of epiphytes and lianas (Puig et al. 1987). Although meteorological data for this site are not available, a nearby station located at 1,100 m records a mean annual temperature of 13.8 ºC and total annual precipitation of 2,522 mm (Puig and Bracho 1987). Distance between study sites is 7.94 Km, being a reflection of the sharp change present on the eastern slopes of ECBR.

Experimental design and trapping.—Since previous research has found seasonal differences in activity patterns (O'Farrell 1974), I restricted my fieldwork to summer months, May to August, of 2001, 2002 and 2003. For logistic reasons I could not sample the CF site in 2003. At each vegetation type sampling sites remained the same

for all years, and they comprised all the different microhabitats present at each area. Each trapping session was carried exclusively within nine-day sampling periods coinciding with new moon phases when activity is presumably highest (Kaufman and Kaufman 1982; Wolfe and Summerlin 1989). These nine-day periods comprised four days before and after a new moon peak night, thus each summer had only 4 trapping periods. For each trapping session, I established one Sherman live trap transect of 150 to 180 traps set 7 mts apart and baited with peanut butter, rolled oats and vanilla extract. All traps were set by 1900 hr and were checked every 2 hrs until 0700 hr (O'Farrell 1974; Cameron et al. 1979; Drickamer and Springer 1998; Vieira and Baumgarten 1995). Approximately 15 to 20 minutes were needed for each session. Traps were left open during the day to detect any diurnal activity, but were not checked until re-baiting in the afternoons. Average sunrise and sunset during the summer months of my study were at 0628 hr and 1950 respectively. At my study site, the maximum deviations experienced during the months of this study were 33 minutes for average sunrise and 36 minutes for average sunset.

Study of activity patterns of small mammals by means of trapping is subject to some bias inherent in methodological protocols, with every method having advantages and disadvantages (Bruseo and Barry 1995; Drickamer and Springer 1998; Hicks et al. 1998; Halle and Weinert 2000). Based on previous studies I implemented two modifications: first, I removed successful traps and replaced them with new ones at each 2-hr revision to maintain trap effort uniform at each time period; and second, I kept trapped individuals because preliminary trials showed that immediate release of captured

rodents could cause biases due to trap-proneness of some individuals (Castro-Arellano pers. obs.). Individuals were processed (identified, weighted, sexed and marked) the next day and were released at their capture site. Since traps were checked at 2-hour intervals, I used trap periods as a more detailed measure of capture effort as in previous works (O'Farrell 1974; Vieira and Baumgarten 1995). Average daily success rate was roughly double in the CF (12.81%) relative to the TSDF (5.96%). Thus, a higher trapping effort was needed in the latter site (5,810 trap nights = 29,050 trap periods) than in the former site (1,040 = 5,200) to acquire sample sizes large enough to perform analyses. Overall, I completed 6,850 night traps that equal 34,250 trap periods.

Data analysis.—Frequency of rodents entering traps was the variable I used to assess the intensity of activity. Since the number of individuals of the same species captured at different periods in the same night was low, I assumed that any effects of shifting population size available during the night were not important enough to affect my results. I first tested whether there was an equal use of each 2-hr night interval by each rodent species at each vegetation site with Chi-square goodness of fit tests. For *Oryzomys couesi* and *Baiomys taylori,* I pooled frequency data in 4-hour intervals to allow for this analysis because of small sample sizes. To test for differences in frequency distribution of captures between each species pair from each forest, I did Kolmogorov-Smirnov two sample tests (K-S), and to assess differences in the central tendency of activity, I used the Mann-Whitney test (M-W). These tests differ in their sensitivities to alternative hypothesis so they can provide complementary views of the data: the null hypothesis for the K-S test is that the two samples are distributed

identically whereas the null hypothesis for the M-W test is that the two samples come from populations having the same location. Thus, the M-W test detects changes in location whereas K-S tests for differences in the entire distributions (Sokal and Rohlf 1995). In addition to these pair-wise comparisons between species at each site, I also performed intra-specific tests between sexes, juveniles versus adults, and years whenever I had sample sizes large enough to perform these tests. I applied Bonferroni corrections for pairwise comparisons whenever needed. I performed all statistical analyses with SPSS version 11 (SPSS 2001) at a significance level of 0.05. Frequencies of first captures of individuals and total number of captures, both pooled at 4 hr intervals to allow analysis, did not differed significantly for any tested species (*P. levipes*, X^2=0.177, d.f.=2, P=0.91; *P. ochraventer*, X^2=0.304, d.f.=2, P>0.86; *P. pectoralis*, X^2=0.687, d.f.=2, P=0.7; *L. irroratus*, X^2=0.018, d.f.=1, P=0.89; *S. hispidus*, X^2=0.358, d.f.=2, P=0.84; *B. taylori* represents first captures only and *O. couesi* had only 3 recaptures) so I assumed that all captures were independent, and analyses were applied to total captures (as in Bruseo and Barry, 1995). Given that the same individual only captured once per night, and only rarely on consecutive nights, the assumption of the independence of the hour of capture for multiple captures of the same individual is reasonable. Further support to this approach comes from the lack of significant differences for both central location and frequency distributions between capture and recapture data for all species (See Table 6).

Null model analyses.—To address overall structure of night use in the TSDF community, I used three different null models that used Monte Carlo simulations for

Table 6.—Comparison of first capture and recapture data of activity patterns of the rodent species at two small mammal communities at El Cielo Biosphere Reserve. *B. taylori* is not included here since data for this species represents first captures only.

species	sample sizes		test statistics			
	First	Recapture	Mann-Whitney U	P	Kolmogorov-Smirnov Z	P
Tropical Subdeciduous Forest community						
Peromyscus pectoralis	101	91	4035.5	0.136	0.583	0.885
Liomys irroratus	29	15	217.0	0.989	0.137	1.000
Oryzomys couesi	21	3	21.0	0.331	0.617	0.841
Sigmodon hispidus	40	34	609.5	0.423	0.536	0.936
Cloud Forest community						
P. levipes	58	19	387.5	0.507	0.651	0.791
P. ochraventer	37	14	197.5	0.184	0.671	0.759

evaluating significance of observed temporal niche overlap. For each model, original data consisted of a matrix represented by species in each row with columns corresponding to each one of the six 2-hr night intervals as a resource state. Entries in the matrix consisted of total number of captures for each species during that night interval. To quantify niche overlap between each species pair, I calculated both the Pianka index (Pianka 1973) and the Czekanowski index (Feinsinger et al. 1981). Both

are symmetric indices that approach 0 for species that do not share resource states and get close to 1.0 for species pairs that have identical resource use distributions. To quantify overlap at the entire community level, I calculated a mean value from all unique species pairs in the assemblage. I compared the significance of observed niche overlap by comparing it with three null models that randomized observed capture frequencies for each species. I used three different kinds of randomization algorithms (RA) to test for non-random temporal niche overlap patterns. I used the RA3 and RA4 algorithms implemented by the software EcoSim (Gotelli and Entsminger 1999) and an ad hoc model (ROSARIO) in a program I developed through modifications of a previously published model (Tokeshi 1986). Both RA3 and RA4 performance has been extensively evaluated with reference data sets (Winemiller and Pianka 1990), and thus for consistency I have kept the same label for each algorithm. As such, my three randomization algorithms are:

RA3. All entries for each row were randomly reshuffled, allowing utilization of any of the resource states in the matrix. I am not aware of any internal restriction (eg., physiological, phylogenetical) in the rodent species I studied that could curtail them from using all resource states in absence of species interactions thus making this model feasible. This is the most "null" of the models I tested, and even though some authors suggest it is not the best option for temporal niche overlap (Albrecht and Gotelli 2001), I included it to serve as a benchmark for comparison against the other two, more realistic models.

RA4. Only the non-zero entries in each row were reshuffled and thus the niche breadth and location of zeros were maintained. Both RA3 and RA4 have the disadvantage of disrupting the shape of activity curves with the possibility of having alternated sequences of highest and lowest frequencies in adjoining intervals in the randomizations (Gotelli and Graves 1996). Nevertheless, RA4 has been reported before to test for diel patterns of temporal niche overlap (Albrecht and Gotelli 2001). Again, I included both of them since they represent increasing levels of algorithm complexity against my ad hoc model.

ROSARIO (ad hoc model). This is a modification of the SONIA model of Tokeshi (1989) to a diel cycle. In this model, the frequency distribution curve of each species was maintained, but randomly arranged along the time axis and rotated in a circular fashion. I generated a set of five random numbers (r1, r2,…., r5), between 0 and 6, and then distribution curves for each of the five species were moved by ri 2-hr intervals from their original position. Since only six nighttime intervals exist, the part of a curve that exceeds the nighttime was automatically relocated to the first night time interval. I named it ROSARIO after the catholic tradition of rosary praying where beads are advanced in a circular fashion. I believe that naming null model algorithms will help avoid literature confusions for future reference.

I randomized my original data set according to these three null models and created 1,000 pseudocommunities for each model. From these I calculated mean niche

overlap of all possible pair-wise comparisons using both Pianka and Czekanowski indices, obtaining two measures of community wide temporal overlap in the null assemblages. By tallying the number of times that simulated niche overlaps were greater or less than its corresponding observed value in the real community, I was able to calculate two-tailed probability values. These indicated if the observed mean niche overlap was more or less than expected by chance alone. In a community where species interactions are driving niche partitioning one expects to find significantly less overlap when compared to the pseudocommunities generated by the simulations.

I excluded CF data from null model analyses since this community is restricted to a single pair of species. The statistical finding that niche overlap in any particular pair of species is lower than expected is hard to evaluate. Historical effects could easily be responsible for this pattern, having nothing to do with species interactions. However, explaining low overlap for several coexisting species would be much more difficult to explain using this simple approach for all possible species pairs (Gotelli and Graves 1996).

RESULTS

I found highly contrasting species compositions, both in terms of identity and diversity, between the two small mammal communities. During trapping for my study, I captured 213 individuals in 357 capture events that represent 10 rodent species at the TSDF site: *Peromyscus pectoralis* (white-ankled mouse), *Sigmodon hispidus* (hispid cotton rat), *Oryzomys couesi* (Coues' rice rat), *Baiomys taylori* (northern pygmy mouse),

Liomys irroratus (Mexican spiny pocket mouse), *Oligoryzomys fulvescens* (pigmy rice rat), *Reithrodontomys mexicanus* (Mexican harvest mouse), *Reithrodontomys megalotis* (Western harvest mouse), *Mus musculus* (house mouse) and *Rattus* sp. (brown rat). Due to differences in abundance, I only obtained large sample sizes for the first 5 species. In contrast, I captured 98 individuals, in 127 capture events, of 3 rodent species and one insectivore at the CF site: *Peromyscus ochraventer* (El Carrizo deer mouse), *Peromyscus levipes* (brush mouse), *Oryzomys chapmani* (Chapmans' rice rat) and *Cryptotis mexicana* (Mexican small eared shrew). The sample sizes I obtained are only large enough for analysis of activity patterns of the first two rodent species. In all species I analyzed from both sites, the number of individuals was always substantially larger than the number of recaptures, which yields confidence that my dataset is an adequate representation of each species activity pattern (Table 6).

Traps were left open during the day but I did not register a single diurnal activity event during all of my study. Most of the species I analyzed from both sites showed a heterogeneous use of the night with only *B. taylori* and *P. ochraventer* being non-significantly different from the null hypothesis expectation of equal activity between night intervals (See Table 7). For *B. taylori* this is probably an artifact of the small sample size and the need to pool captures in 4-hr intervals for analysis. Instead, *P. ochraventer* did indeed show a tendency towards a uniform activity pattern through the night, although this was only marginally non-significant (Table 7) as there was some drop in activity towards dawn. Other species showed clear peaks in activity at some point during the night.

Table 7.—Chi-square Goodness of Fit test results for activity patterns of species from two small mammal communities at El Cielo Biosphere Reserve. Null hypothesis tested is for equal activity between the six 2-hr night slots. Due to small sample sizes, tests for *Baiomys taylori* and *Oryzomys couesi* are for 4 hr intervals.

species	sample size	test statistic	df	P
Tropical Subdeciduous Forest community				
Peromyscus pectoralis	192	42.313	5	<0.001
Liomys irroratus	44	58.273	5	<0.001
Oryzomys couesi	24	25.375	2	<0.001
Sigmodon hispidus	74	41.459	5	<0.001
Baiomys taylori	15	2.800	2	0.2466
Cloud Forest community				
P. levipes	73	13.712	5	0.018
P. ochraventer	51	10.529	5	0.062

Not all species used the night in the same way, with some pairs showing remarkable similarities or differences in their patterns (Figures 9 and 10). At the TSDF, both *S. hispidus* and *B. taylori*, showed a bimodal pattern with a marked tendency towards crepuscular activity and reduced levels of activity in the middle of the night. In contrast, *L. irroratus* and *O. couesi* showed almost completely opposite patterns with *O.*

couesi using earlier parts of the night with a peak between 2100 and 2300 hr, whereas the highest activity of *L. irroratus* occurred between 0300 and 0500 hr (Figure 9). In this same community, *P. pectoralis* showed a unimodal activity pattern with a peak between 2100 and 2300 hr with a gradually decreasing towards sunrise. At the CF community, both species of *Peromyscus* had relatively similar activity patterns with more activity earlier in the night and gradual decreases afterwards. However, *P. ochraventer* had its activity peak between 1900 and 2100 hr, whereas *P. levipes* highest activity was in the subsequent 2-hr interval (Figure 10). Secondary peaks of activity occur in both species, with *P. ochraventer* again having it earlier, 0100-0300 hr, than P. levipes, 0300-0500 hr.

My pair-wise tests of mean and frequency distributions of activity for species at the TSDF reveal that half of the species pairs show significant differences in their night use patterns (Table 8). Both *P. pectoralis* and *L. irroratus* had a pattern significantly different from all other species in this community, with the exception of *B. taylori* which showed no differences with any other species in the community. Interestingly, *P. pectoralis* and *L. irroratus* had significant differences in their mean hour of activity, but had marginally non-significant differences in the frequency distribution of their captures. This result stresses the need to use both the Mann-Whitney and the Kolmogorov-Smirnov tests since each one provides a different view of the data. At the CF site *P. ochraventer* and *P. levipes* showed no differences in either their mean hour of activity (M-W U=1677.5, P=.340) or frequency distribution of captures (K-S Z=.824, P=.505).

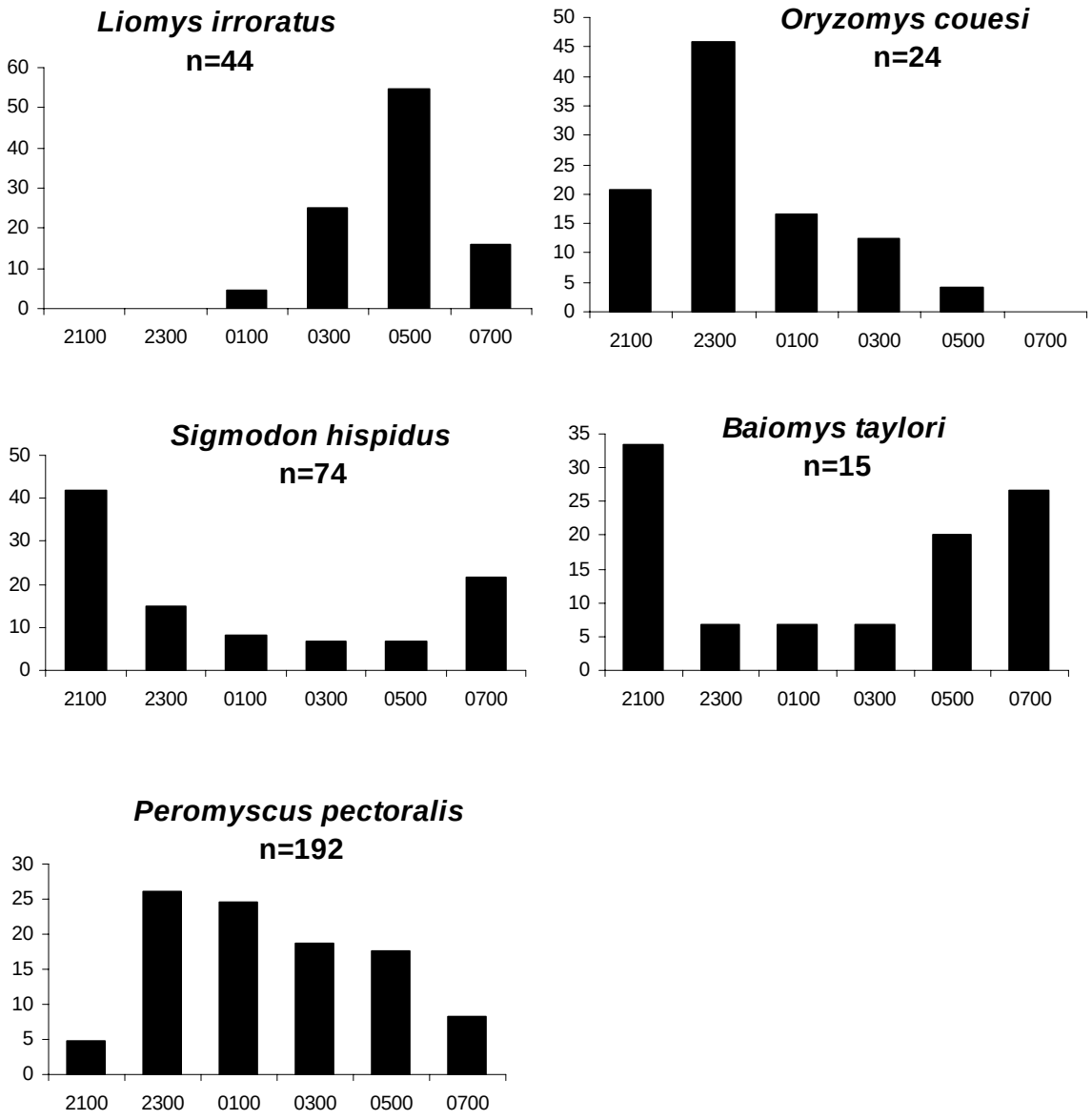

Figure 9.—Percentage of activity for the most abundant rodent species at the Tropical Subdeciduous Forest community from El Cielo Biosphere Reserve, Tamaulipas, Mexico. The Y axis denotes percentage of captures during all the study and the X-axis denotes the times at which traps were checked during the night, thus representing activity within the previous 2 hrs (see text for details).

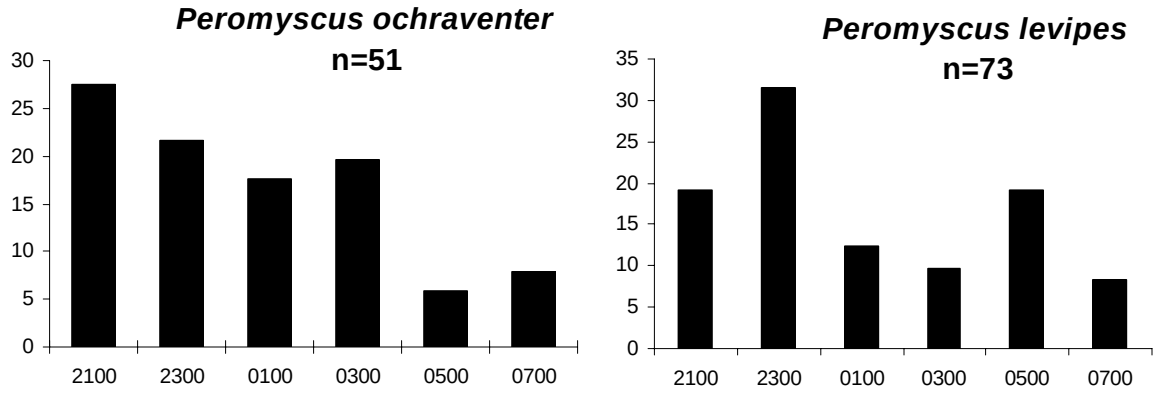

Figure 10.—Percentage of activity for the most abundant rodent species at the Cloud Forest community from El Cielo Biosphere Reserve, Tamaulipas, Mexico. The Y axis denotes percentage of captures during all the study and the X-axis denotes the times at which traps were checked during the night, thus representing activity within the previous 2 hrs (see text for details).

For all species in both communities, I found no significant differences between male and female activity patterns in either mean hour of activity or frequency distribution of captures (Table 9). In one TSDF species, *Sigmodon hispidus*, I found a significant difference in mean activity times between males and females when all captures are considered in the analysis. Males had a higher mean rank value (41.69) against that of females (31.69). When only first captures are considered, this difference between sexes disappears (Table 9). A revision of my capture database revealed that while male recaptured individuals were trapped again in the same time interval (or at least in the same half of the night), females were recaptured at earlier times than their original capture, introducing a bias in the analyses when all captures are considered. It is

Table 8.—Pairwise interespecific comparisons of activity for species at the Tropical Subdeciduous Forest community. To maintain an overall alpha of 0.05 the significance level for individual comparisons is 0.005 due to the Bonferroni correction. U = Mann-Whitney U statistic; Z = Kolmogorov-Smirnov Z statistic. PI = Pianka's niche overlap index. CI = Czekanowski overlap index.

	n = 44		n = 24		n = 74		n = 15	
	L. irroratus	P	*O. couesi*	P	*S. hispidus*	P	*B. taylori*	P
n = 192								
Peromyscus pectoralis	U = 1815	<0.001	U = 1257.5	<0.001	U = 5367.5	0.002	U = 1404	0.869
	Z = 3.031	<0.001	Z = 1.66	0.008	Z = 2.719	<0.001	Z = 1.068	0.204
	PI = 0.598		PI = 0.814		PI = 0.525		PI = 0.545	
	CI = 0.493		CI = 0.641		CI = 0.495		CI = 0.507	
Liomys irroratus			U = 51.5	<0.001	U = 816.5	<0.001	U = 245.5	0.119
			Z = 3.105	<0.001	Z = 3.169	<0.001	Z = 1.409	0.038
			PI = 0.18		PI = 0.289		PI = 0.566	
			CI = 0.212		CI = 0.340		CI = 0.471	
Oryzomys couesi					U = 886	0.851	U = 131	0.147
					Z = 1.031	0.239	Z = 1.291	0.071
					PI = 0.646		PI = 0.481	
					CI = 0.547		CI = 0.450	
Sigmodon hispidus							U = 470	0.331
							Z = .646	0.798
							PI = 0.931	
							CI = 0.817	

Table 9.—Intraespecific gender comparisons of activity patterns for two small mammal communities at El Cielo Biosphere Reserve. AC=all captures considered; FC=first captures only. Data for *B. taylori* consists of only first captures.

species		sample sizes		test statistics			
		Female	Male	Mann-Whitney U	P	Kolmogorov-Smirnov Z	P
Tropical Subdeciduous Forest community							
Peromyscus pectoralis	AC	76	111	3985.5	0.513	0.76	0.611
	FC	37	61	1042.5	0.518	0.744	0.637
Liomys irroratus	AC	17	26	169.0	0.150	0.544	0.929
	FC	12	16	92.5	0.857	0.164	1.000
Oryzomys couesi	AC	9	14	50.0	0.382	0.743	0.639
	FC	8	12	42.5	0.678	0.456	0.985
Sigmodon hispidus	AC	31	43	486.5	0.039	1.181	0.123
	FC	18	22	153.0	0.196	0.922	0.364
Baiomys taylori	FC	8	7	26.0	0.811	0.656	0.783
Cloud Forest community							
P. levipes	AC	28	44	546	0.408	0.685	0.736
	FC	26	32	331.5	0.175	0.91	0.378
P. ochraventer	AC	23	27	190	0.016	0.993	0.277
	FC	19	17	108	0.084	0.872	0.433

worth noting is that this bias in recapture data only occurred in one species. All other species showed non-significant differences between males and females with either all data or first capture data, highlighting the consistency of activity patterns within species. Comparisons of activity patterns between juveniles and adults, and between years further demonstrate the intraspecific consistency of activity patterns. In the TSDF only *P. pectoralis* had enough captures to compare juvenile (n=29) and adult (n=163) activity patterns. I found no significant differences between them in either mean hour of activity (M-W U=2156.5, P=.442) or frequency distribution of captures (K-S Z=.896, P=.398). Other species at this site had two or less captures of juvenile individuals, preventing any comparisons with adults. At the CF site, I did not capture any juveniles for either of the *Peromyscus* species analyzed. In addition to the lack of differences between sexes and age stages, I found no evidence of significant changes in activity patterns between years for either the TSDF or CF sites (Table 10). Rodent species at the TSDF had a mean niche overlap of 0.558 with pair-wise values ranging from 0.18 to 0.931 with Pianka's index and from 0.212 to 0.817 with Czekanowski index (Table 8). The highest overlap was between *S. hispidus* and *B. taylori,* whereas the least overlap occurred between *L. irroratus* and *O. couesi* (Figure 9).

In the null model tests each randomization algorithm provided different results, with an obvious trend in significance level from the "nullest" to the more complex model (Table 11). A sequence of decreasing probability of finding an equal or lower mean overlap between the observed mean from the null model simulations and the

Table 10.—Between years comparisons of activity patterns for two small mammal communities at El Cielo Biosphere Reserve. Only years with 15 captures of more are included in this table. To maintain an overall alpha of 0.05 the significance level for between year comparisons for *Peromyscus pectoralis* data is 0.016 due to Bonferroni correction. Analysis of first capture only data for these comparsions yielded non-significant results in all cases.

species		sample sizes			test statistics			
		2001	2002	2003	Mann-Whitney U	P	Kolmogorov-Smirnov Z	P
Tropical Subdeciduous Forest community								
Peromyscus pectoralis								
	2001 vs 2002	24	67	---	636.5	0.121	0.907	0.383
	2001 vs 2003	24	---	101	1136.5	0.628	0.678	0.748
	2002 vs 2003	---	67	101	3000.0	0.204	0.747	0.633
Sigmodon hispidus								
	2002 vs 2003	---	29	39	547.5	0.815	0.764	0.603
Cloud Forest community								
P. levipes								
	2001 vs 2002	18	55	---	476.0	0.803	0.346	1.000
P. ochraventer								
	2001 vs 2002	16	35	---	246.5	0.487	0.485	0.973

Table 11.—Observed and expected mean temporal niche overlap for the three different randomization algorithms. Expected values are calculated from niche overlap indices of 1,000 randomly assembled communities. See text for description of randomization algorithms (RA3, RA4, ROSARIO). Tail probability corresponds to the probability of observing a mean overlap equal or smaller, than then mean from the real community, in the simulations. PI = Pianka's niche overlap index. CI = Czekanowski overlap index.

Model	index	Observed mean niche overlap	Expected mean niche overlap	Tail Probability
RA3	PI	0.56	0.62	0.068
	CI	0.50	0.55	0.008
RA4	PI	0.56	0.62	0.072
	CI	0.50	0.55	0.018
ROSARIO	PI	0.56	0.62	0.084
	CI	0.50	0.55	0.026

observed mean in the real community goes from RA3 to RA4 to ROSARIO. For the Czekanowski index this trend was very evident from the very low probability for the RA3 model to a larger, but still significant, value for the ROSARIO model. Instead, for Pianka's index the probabilities did show the same trend but variation was much more restricted with very similar probability values that were marginally non-significant in all cases.

DISCUSSION

Statistical analyses of individual diel patterns show that the activity pattern was highly consistent within each species and did not change across sex, age class and years. Such consistency makes diel rhythms well suited for their inclusion in studies of community ecology and resource use. I found strong evidence of non-random temporal niche partitioning in the small mammal community at a TSDF site, in contrast to the CF community where temporal segregation was non-existent. Null model results for the TSDF depended on the model and index used but the ROSARIO model using the Czekanowski index provided the most adequate combination to reach conclusions about temporal partitioning at this community. The ROSARIO model is the most biologically realistic model since it maintains the frequency distribution curve of each species (Gotelli and Graves 1996). It provides the most rigorous test for detection of non-randomness in temporal niche partitioning for the whole community. However, the probability of observing a mean overlap equal or smaller than the mean overlap from the real community in the simulations also depended on what index was used. Given a significance level of 0.05, if Pianka's index is used then the result is marginally non-significant whereas with the Czekanowski index the result is significant. Some researchers consider index election to be a rather subjective matter (N. Gotelli, personal communication) but in this case the performance of both indices can be contrasted by comparing results for each of the tested null models. The increased complexity in the three null models, RA3, RA4 and ROSARIO, show a correlated increase in the null space that ideally should be mirrored by tail probability values independent of which

overlap index is used. RA3, the most "null" of the algorithms, was expected *a priori* to provide smaller probability values since this algorithm produces a higher number of combinations by entirely reshuffling all data in each row, thus creating a very large null space. On the other hand, since the ROSARIO model reshuffles data in the most restricted way, I expected to see comparatively higher probabilities with this model. Response to these model assumptions was substantially different for the two indices. The Czekanowski index showed marked differences in this tail probability between null models (0.008 to 0.026) whereas Pianka's index variation was much lower (0.068 to 0.084). The Czekanowski index is more able to represent these differences in model assumptions and thus is a more adequate index for this analysis. Additionally, this index has the benefit that it can be graphically interpreted as the correspondence to the area of intersection of utilization histograms of the two species under comparison. Overall, the Czekanowski index is a better descriptor of temporal overlap and thus well suited to reach conclusions about temporal partitioning at the TSDF community.

As shown by these null model analyses, the probability of observing this structure by chance alone is small, so a mechanistic explanation is likely behind this pattern. Care should be taken to avoid falling immediately into a traditional but poorly sustained dogmatic explanation in which a single process, ie. competition, is assumed as the major or only force structuring this small mammal assemblage. I do not claim to have estimated inter-specific competition directly from the temporal niche overlap but rather I am showing evidence of a statistically significant segregation pattern. My statistical evidence of temporal community structure is best viewed as a basis to

formulate hypotheses that should be tested with experimental studies, which can provide evidence for any postulated process. Other phenomena, besides competition, such as predator-induced segregation and historical (phylogenetic) factors, could also be addressed as possible explanations. In my study system, additional insight into possible mechanistic causes for temporal structure, or lack of it, can be derived from ancillary data I have collected (Chapter IV) and from natural history information of rodent species in these assemblages.

As part of a concomitant study of microhabitat use by small mammals in the ECBR, I found that the TSDF community can be subdivided into two groups, with *P. pectoralis* occurring mainly in closed forest zones against remaining species that used mostly ecotone and open areas (Chapter IV). Pooling captures at each microhabitat makes evident a striking pattern where open area species avoided activity in middle-night intervals whereas the single closed forest species showed an activity peak during this time (Figure 11). This contrast is partially responsible for creating the significant result in my null model analysis and as such is highly relevant to considerations of a mechanistic explanation in the overall structure in the community. I hypothesize that ecotone/open area species might have a predator mediated effect that constraints use of certain night intervals (Kotler et al. 2002; Fraser et al. 2004). Several species of owls are know to occur in ECBR, being the Ferruginous Pygmy-Owl, *Glaucidium brasilianum*, the Tamaulipas Pygmy-Owl, *Glaucidium sanchezi*, and the Mottled Owl, *Ciccaba virgata*, the most likely nocturnal predators of rodents at the TSDF and CF communities (Howell and Webb 1995; Arvin 2001). Potentially, predation presents a higher risk in

open areas during certain night intervals, and as such, activity during those times may be avoided by species using these areas (Jacob and Brown 2000). It is very plausible that community structure is not being driven by exploitative competition of food or space but for competition of "enemy-free space" instead (Jeffries and Lawton 1984). Additionally, phylogenetic constraints of constituent species are another possible cause for this division of activity patterns between microhabitats. Both *B. taylori* and *S. hispidus* have been previously reported as crepuscular species as in my study (Cameron and Spencer 1981; Eshelman and Cameron 1987). Furthermore, in another study *S. hispidus* failed to change its diel activity pattern even after a presumed competitor was experimentally removed (Cameron et al. 1979). So, it is plausible to think that these species with open area microhabitat preferences may have evolved specific activity pattern strategies which now represent evolutionary constraints (Kronfeld-Schor et al. 2001). If this hypothesis were correct, their contribution to produce a lower community temporal niche overlap would be mediated by the interplay of microhabitat selection and evolution of diel rhythms. Determining whether diel activity patterns in these species are significantly associated with position in a phylogeny will provide an insight into this hypothesis. A study that includes all these syntopic species in a phylogeny would be able to discern whether assembly is formed by phylogenetically unrelated taxa with complementary diel patterns, or by closely related taxa with a divergent pattern, that have separated through an adaptive-radiation-like process driven by competition and ecological segregation. Carefully designed comparative studies of this kind with other

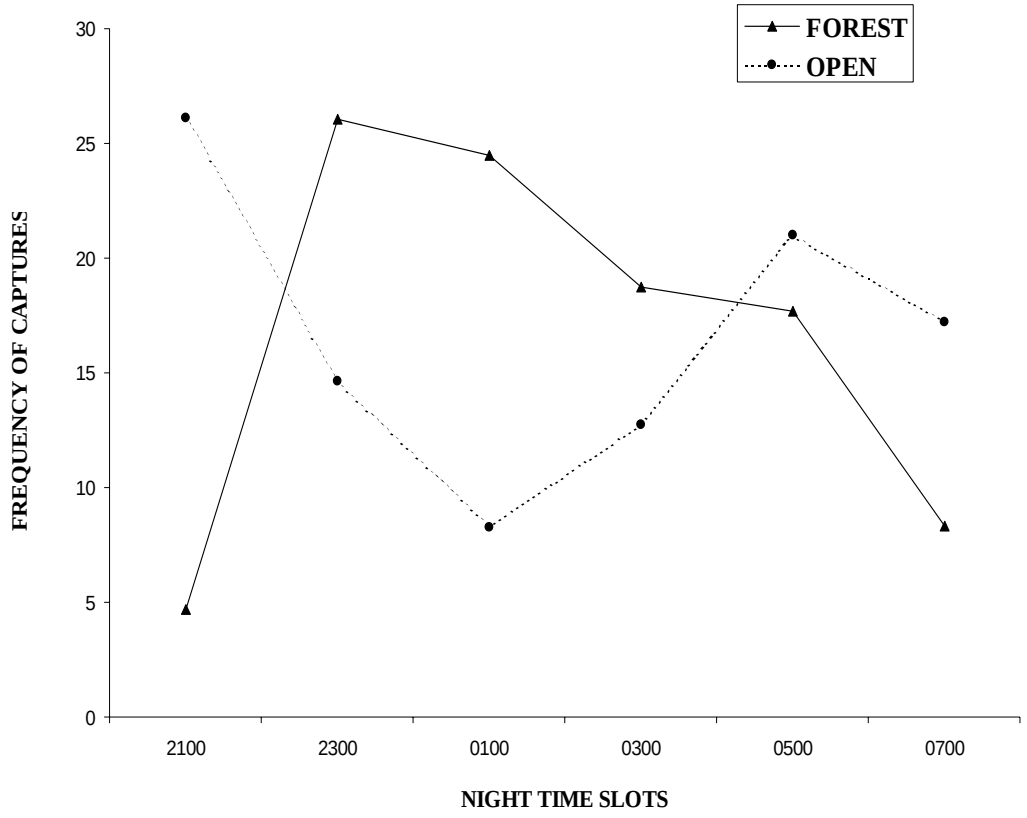

Figure 11.—Comparison of pooled activities between species in open/ecotone microhabitats against the single closed forest microhabitat species (*Peromyscus pectoralis*). See discussion for explanation.

communities would provide a confirmation and generality of this hypothesis.

An even more interesting pair of species from the TSDF community that also occupies the ecotone/open areas is that of *L. irroratus* and *O. couesi*. This species pair had the lowest temporal overlap because of an almost opposite activity pattern and had no differences in their microhabitat use preferences (Chapter IV) thus providing a perfect example of niche complementarity. Unfortunately, nothing is known about their

activity patterns in other communities since my study represents the first report of their diel rhythms and so I cannot make inferences on whether their activity represents an aberrant or normal pattern. In an analysis of fitness between the hypothetical costs of activity and inactivity Daan and Aschoff (1982) suggested that an optimum time for activity onset in small mammals would be situated at the start of the night. In this scheme a species that comes later in the night to forage would be incurring in higher fitness costs than one with an earlier activity pattern. Competitively induced shifts in activity patterns have been experimentally demonstrated for some small mammal pairs where one species is pushed to a less adequate activity time by a more dominant species (Shkolnik 1971; Ziv et al. 1993). As has been shown in one of these systems an understanding of the nature and dynamics of shared limiting resources becomes crucial to ascertain mechanisms responsible for temporal partitioning in allowing coexistence of species at a given community (Ben Natan et al. 2004). Interestingly, both of these competing small mammal pairs are congeners whereas in my study they represent not only different genera but also even families. Closely related species are expected to have similar constraints in resource use, but this is not the case for phylogenetically separated species. Two different hypotheses that can explain the extreme temporal niche separation in this species pair can be derived: a convergent use of a locally abundant resources coupled with an aggressive interference competition, and "enemy free space" competition from a shared predator(s) (Jeffries and Lawton 1984).

Moreover, an assessment of the distribution of body sizes in both TSDF and CF rodent communities might not only expand the previous hypothesis for the extreme

separation of *L. irroratus* and *O. couesi,* but could even explain further structural features at both TSDF and CF assemblages. It has been shown that species with similar body weights experience similar energetic constraints and that body size structure in some rodent communities does not follow random patterns, thus claiming competitive exclusion of similar sized species having a role in community assembly rules (Brown 1998; Weiher and Keddy 1999). As such, one would expect to find that syntopic, similarly sized species partition their resources along other niche axes such as time. This could also provide a plausible explanation for the separation of *L. irroratus* and *O. couesi* since they are very similarly sized species (body mass ratio of 1.1). Moreover, the largest overlap in activity pattern between *S. hispidus* and *B. taylori* corresponds to the largest difference in size (body mass ratio of 8.24). Finally, in the CF both species of *Peromyscus* showed no activity pattern differences and also overlapped greatly in microhabitat use (Chapter IV) but were moderately different in size (body mass ratio of 1.5). Whether these body mass distributions are the product of mechanistic processes or just random distributions remains to be tested. A counterargument to this hypothesis is that similarly sized rodent species might be using different food resources, thus allowing for coexistence. There is no quantitative report available that could either confirm or refute this prediction. Given the apparent variability in diet for these or similar species (Reid 1997; Villa and Cervantes 2003) I am more inclined to think that, within my system, time is a more important niche axis than food albeit this issue needs to be confirmed with further investigation.

The issues addressed by this study are broader than simply the temporal activity patterns between rodent species at two contrasting communities of a subtropical zone. The interplay of competition, predation, microhabitat, use and evolution of diel rhythms that has been shown to be important for the understanding of relative simple communities, eg. desert rodents (Kronfeld-Schor and Dayan 2003), is not as extensively documented for more diverse tropical communities. Ecological theory would benefit greatly with careful comparative studies of structurally complex tropical sites that harbor higher species numbers.

CHAPTER IV

MICROHABITAT USE AT TWO CONTRASTING COMMUNITIES IN EL CIELO RESERVE

Small mammals have been used as model organisms for an extensive body of research that has influenced vertebrate terrestrial community ecologists (Brown and Harney 1993). Studies of small mammals have given rise to the paradigm that differential use of microhabitat enables coexistence of sympatric species in this group of mammals (Reichman and Price 1993). However, the universal validity of this paradigm has recently been questioned because of the lack of uniformity and strength of its empirical foundations (Jorgensen 2004). In a survey of 70 published studies, Jorgensen (2004) found lack of consistency in the spatial definition and measurement of microhabitats, low number of vegetation types addressed at each study, modest trapping efforts (<5,000 trapnights), and concentration of studies in a few species (50% of studies pertained to only 8 species). This author suggests that this concentration of knowledge is an insufficient foundation to claim that microhabitat partitioning is the major model enabling coexistence of sympatric species.

In spite of extensive studies that have documented patterns of segregation of small mammals species into structurally distinct microhabitats for both neartic forests (Dueser and Shugart 1978; Morris 1996) and desert rodents in south west North America (Brown and Harney 1993; Heske et al. 1994), there are other studies that do not support the microhabitat paradigm (Bowers 1986; Morris 1987; Jorgensen and Demarais 1999). Therefore, the issue is far from settled. Nevertheless, the general notion that the

microhabitat paradigm is correct has lead to a trend toward less interest in this type of research (Jorgensen 2004). This recent review clearly shows the need for continued efforts in this area. Even more compelling is the fact that all of the studies that were the basis of this review dealt with small mammal communities in the neartic region. Detailed studies about microhabitat use in tropical and subtropical small mammal assemblages from the neotropics are fewer than their neartic counterparts (Lacher and Mares 1986). Given the structurally more complex nature of some neotropical environments (August 1983) they can potentially provide additional information compared to more simple neartic systems. Recently published work in the neotropics (Lacher and Alho 1989; Lozada et al. 2000; Lacher and Alho 2001; Vieira 2003) indicate that is still being conducted, for this less well known environments, however, a detailed review such as the one done for the neartic communities (Jorgensen 2004) would be useful to assess the current state of our knowledge in these habitats. Combined microhabitat research at both neartic and neotropical regions will provide an opportunity to verify the generality of any pattern.

In the present chapter I address the microhabitat use patterns for small mammals species at both the TSDF and CF communities at ECBR. The elevational gradient changes at this reserve, located over a transition zone between the Neartics and the Neotropics, allows for the unique opportunity to compare contrasting communities adjacent to each other (Martin 1955; Martin 1958), thus eliminating the effect of large historical difference such as the ones expected in comparisons made between distantly occurring communities (Lacher and Mares 1986). For my study I use measurements of

11 variables at a very fine scale to test for the null hypothesis of no differences in microhabitat use between species. I contrast my results from this chapter with the conclusion derived from previous chapters in order to gain a further insight of the ECBR small mammal assemblages.

MATERIALS AND METHODS

Study area.—I conducted my study as part of a larger project about rodent community dynamics at El Cielo Biosphere Reserve (Chapters II and III). This reserve encompasses approximately 144, 500 ha in southwestern Tamaulipas, Mexico. A sharp altitudinal gradient is present in the eastern part of the Reserve with a pronounced change in elevation of 200 to 1,800 meters. Three different vegetation zones occur over this gradient inside the reserve: Tropical Subdeciduous Forest (TSDF), Cloud Forest (CF) and Pine-Oak Forest (POF). I conducted my fieldwork in the southeast portion of the Reserve within the limits of Gomez Farias municipality (23 03'42" N and 99 12'18" W). At the TSDF sites the dominant species at canopy level were *Bursera simaruba*, *Brosium alicastrum*, *Lysiloma divaricata*, *Mirandaceltis monoica*, *Croton niveus*, *Savia sessiliflora*, *Drypetes lateliflora*, *Acalypha schiedeana*, and *Ficus* spp. (Sosa 1987; Valiente-Banuet et al. 1995). The understory of this forest has *Acalypha schiedeana*, *Urera caracasana*, *Chamedorea radicalis* and *Syngonium podophyllum* as prevailing species (Valiente-Banuet et al. 1995). Within this vegetation type there are open areas, both natural and man-made, where common plants are *Mirabilis jalapa*, *Jacobinia incana*, *Gibasis pellucida*, *Paspalum paniculatum*, *Cenchrus echinatus*, *Argemone*

mexicana, *Sclerocarpus uniserialis* and *Canna indica* among others (Mora et al. 1997). Average elevation at these sites was 300 m with a mean annual temperature of 22.8 ºC and a total annual precipitation of 1,852 mm (Puig and Bracho 1987). In high contrast, the CF sites were at an average elevation of 1,320 m where dominant canopy species were *Liquidambar styraciflua*, *Quercus sartorii*, *Q. germana*, *Clethra pringlei*, *Magnolia shciedeana*, *Podocarpus reichei*, *Acer skutchii*, *Carya ovata* and *Cercis canadensis* (Puig et al. 1987). In this forest the lower strata is codominated by *Ternstroemia sylvatica*, *Meliosma oaxacana* and *Eugenia capuli*, with common presence of epiphytes and lianas (Puig et al. 1987). Although meteorological data for the exact elevation of my sites is not available, a nearby station located at 1,100 m records a mean annual temperature of 13.8 ºC and total annual precipitation of 2,522.4 mm (Puig and Bracho 1987). Distance between center points of study sites from each vegetation type is 7.94 Km, being a reflection of the sharp change present at the eastern slopes of ECBR.

Each forest type not only had very different constituent species, but also a distinctive physiognomy when groups of sampling sites I sampled were compared. The TSDF sites had sharp ecotones that divided relatively flat open areas occupied by grassy and secondary vegetation zones from closed mature forest occurring on rocky hillsides. In contrast, CF sites presented more continuous units either on relatively flat or inclined zones. At this forest most trapping sites had small openings without sharply defined ecotones with only two sites occurring partially within a large opening with short grass and shrubby vegetation in it. Occurrences of open areas in both forest types have been subject to human and natural disturbances. The ECBR is located within a coastal zone

with a high incidence of hurricanes and tropical storms coming from the Gulf of México that result in a high level of natural disturbance over long temporal scales (Arriaga 1987; Valiente-Banuet et al. 1995). Additionally, before the reserve was decreed, logging activities were intensive until the mid-70's where all exploitation ceased (Vargas-Contreras and Hernandez-Huerta 2001).

Trapping design.— I did my fieldwork during the summer months, May to August, of 2001, 2002 and 2003. At each vegetation type we used four different sites to sample each rodent community. One site at each vegetation association was trapped every year whereas the rest were not repeated between summers. For logistic reasons I could not sample CF sites in 2003. Distance between sites within each vegetation type ranged from 1 to 2.5 Km and roughly had the same altitude and slope aspect. For each trapping session I established one Sherman live trap transect of 150 to 180 trap stations set 7 mts apart and baited with peanut butter, rolled oats and vanilla extract. Each station had one trap always placed on the floor since the aim for these transects was to uncover patterns of microhabitat use of rodent species; I referred to as microhabitat transects. I used additional transects to detect scansorial activity rodent species at both forests I sampled (see below). Transects were active from three to six nights in a row with traps set by 1900 hr and checked usually until the next day. On some nights I checked traps every 2-hrs until 0070, as part of a concomitant study of activity patterns for rodent species at these communities (Chapter III). I restricted these nightly revisions to the pair of sites, one at each forest type, which remained the same for the entire study. Captured individuals were identified, weighted, sexed and marked and released at their

capture sites. For each initial capture of every individual I identified the trap station with a wire flag marker, and after trap transects were removed these markers served as reference points to measure microhabitat features.

To detect the scansorial activity of rodent species, I set additional transects arranged differently; I referred to as vertical transects. These transects consisted of 15 to 25 stations, of two traps each, and were always within areas of canopy cover of >80%. At each station I placed two traps: one on the floor, and another one right above the first one was attached to any part of the vegetation (vines, shrubs, tree branches, fallen trees, etc.) with the aid of wide rubber bands. The trap located in the vegetation layer had the door always facing the shortest distance to the floor, and the maximum height I used was around 3 m. Distance between stations varied between 7 m to 10 m and bait was the same one as the used for the microhabitat transects. During the study I collected a representative set of individuals that I prepared as voucher specimens. Vouchers are deposited at the Texas Cooperative Wildlife Collection (TCWC), Texas A&M University and Museo de Historia Natural de Tamaulipas in Ciudad Victoria Tamaulipas. Since a specific key for the small mammals of this area is not available, I identified specimens with the aid of several sources (Cameron and Spencer 1981; Hall 1981; Lackey et al. 1985; Eshelman and Cameron 1987; Davis and Schmidly 1994; Reid 1997; Villa and Cervantes 2003) and with comparisons of reference specimens deposited at the TCWC. For two species of the genus *Peromyscus* I used an additional method of identification based on comparison of cytochrome *b* sequences to reference material (Chapter II).

Vegetation and data analysis.— My main interest was to determine habitat use at a fine scale for each one of the small mammal species I detected at each vegetation type. As such, for each first capture I measured 11 microhabitat variables (Table 12) of the trap station in order to have a quantitative description of structure where each individual was captured. I measured canopy density with the aid of a spherical densiometer (Lemmon 1957) and for distances to structural features I used either a standard measuring tape (<15 m) or an optical rangefinder (>15 m). Since visual estimation of coverage percentages are prone to bias (Kercher et al. 2003) I standardized data collection by using a reference rope over each trap station to be measured. This rope consisted of four 3-m long pieces joined at one extreme, with fluorescent markings every 30 cm. After I centered this rope over the trap station and oriented it, with the aid of a handheld compass, I used it as reference to estimate percentages of ground cover. By counting the number of fluorescent markings touching different cover features (vascular plants, rocks and bare soil) and dividing by the total, I had a non-biased estimate of each cover type. The reference rope also facilitated the delineation of quadrants needed for point quarter method measurements (Pollard 1971; Krebs 1999). My preliminary analyses showed that significant intercorrelations between habitat variables existed. I pooled all successful trap stations for all transects for each vegetation type and ran a Principal Components Analysis (PCA) for both of them. Only abundant species (>3 individuals) were included in the analyses.

Table 12.—Description of microhabitat variables used at each of the two communities. For a better description of how microhabitat variables were measured see methods section.

1. Canopy cover. Mean of four measurements, one for each cardinal direction taken with a densiometer.
2. Tree density (>10 cm DBH) calculated by the point quarter method. Expressed as trees per hectare.
3. Shrub density (woody and <10 cm DBH) density calculated by the point quarter method. Expressed as shrub per m2.
4. Number of log or stumps in a 3 m radius of the trap site.
5. Litter density. Classes were: 0 = null, 1 = scarce, 2 = intermediate, and 3 = abundant.
6. Percentage of bare soil. Determined by counting number of markings over a reference rope touching bare soil and then calculating percentage.
7. Percentage of vascular plants (non-woody). Determined the same way as variable 6.
8. Percentage of large rocks (>30 cm or larger). Determined the same way as variable 6.
9. Percentage of shrub cover. Determined by counting number of markings over a reference rope that were under direct cover of a shrub.
10. Rocky outcrop. Distance in m to the nearest rocky outcrop.
11. Slope. Slope within 3 m radius of the trap site. Classes were: 0-9 = 1, 10-19 = 2, 20-29 = 3, 30-39 = 4, >40 = 5.

The factor scores for all sites on the first six (TSDF) and five (CF) principal components were saved as new variables therefore eliminating the problem of intercorrelation. I grouped trap stations by the species captured, thus creating one group for each of the detected species at each vegetation type. I calculated the mean score for each of the six (TSDF) or five (CF) factors over the number of trap stations for that group. So, each species had a mean factor score for each of the six (TSDF) or five (CF) factors. To assess the similarity in microhabitat use between the species at each vegetation type I did a cluster analysis using the mean scores via an average linkage method. The distance measure that I used was the squared Euclidean distance since all variables were measured using the same scale (factor scores). Species clusters served as a guide to test for differences between groups, within groups, and or species. Given that a large number of pair wise tests are possible, both between groups and species, I restricted these tests to only the ones relevant for contrast with the findings from Chapter III (see Table 8).

I was especially interested to test for differences between the species pairs that had the highest (*B. taylori* and *S. hispidus*), and the lowest (*L. irroratus* and *O. couesi*) overlaps in temporal niche axis in the TSDF, as well as both *Peromyscus* species from the CF. To test for these differences I used multivariate analysis of variance (MANOVA), as well as Kruskal-Wallis and Mann-Whitney tests for variables that did not conform to the assumptions of parametric tests. For both vegetation types, many of the original variables were non-normal, so I used the Box-Cox transformation to correct for normality (Johnson and Wichern 1998). The variables expressed in percentages like

canopy cover and ground cover structure (vascular plants, bare soil, etc.) were analyzed with the non-parametric tests mentioned above.

Finally, I compared capture frequencies between floor and vegetation level traps between syntopic species with a Chi-square test of independence in a 2x2 contingency table. Additionally, for each abundant species captured in the vertical transects I used the Chi-square goodness of fit test to test for the hypothesis of equal use of floor and vegetation layers. I performed all the statistical analyses in SPSS, version 11 (SPSS 2001), and Minitab, version 14 (Minitab 2004), software packages at a significance level of 0.05.

RESULTS

Trapping results.— For the microhabitat transects I did a total of 14,880 trapnights divided between the TSDF (11,260) and the CF (3,620). Overall trapping success for these transects at each vegetation type was 5.62% and 8.70% respectively (Table 13). I detected a total of 11 species at the TSDF and 7 species at the CF (Tables 14 and 15). Two of the species at the TSDF represent introduced species (*Mus musculus* and *Rattus* sp.) and were not included in any of the analyses. At the CF sites two of the species that I trapped are insectivores and 5 are rodents. The single record of the insectivore *Sorex sausurrei* is the first record for ECBR and also the second one for all the state of Tamaulipas. At the TSDF a clear trend from 2001 to 2003 was observed in the number of individuals and species captured (Table 14), and even thought I applied more trapping effort in the last year (Table 13) the trapping success rates also show an

ascending trend being roughly double each new summer. At the CF trapping effort was more constant and the number of trapped individuals was exactly the same. Total species richness only changed by one between years (Table 15). Most of the first captures had their microhabitat data recorded except for a few instances where some transects were disturbed by local people and/or tourists that removed the markers before the data was recorded (see data in Tables 14 and 15).

For the vertical transects total trapping effort added to 1,732 trapnights divided between the TSDF (1,030) and CF (702) sites. Overall trapping success of these transects was 14.85% and 26.35% respectively for each forest. Trapping success of vertical transects against microhabitat transects was higher at both forests: 1.6 times at the TSDF and 2 times at the CF (see Table 13). Vertical transects detected three species in the TSDF and five in the CF (Table 16).

Microhabitat structure analyses.— In the TSDF the first 6 axes extracted by the PCA accounted for 87% of the variance in microhabitat structure among successful trap locations (Table 17). High correlations between variables existed in this dataset. All basic tests that indicate the appropriateness of a PCA supported the analysis (Kaisen-Meyer-Olkin, KMO, measure of sampling adequacy = 0.740, Bartlett's test of sphericity = 2350.14, $P<0.0001$). Factor 1 separated the closed canopy, litter dense areas from the open canopy/litter scarce stations. Factor 2 separated microhabitats on the basis of shrub density and ground cover of bare soil and rocks. Factor 3 separated stations by number of logs or stumps around the trap station as well as the slope. The next three factors are

Table 13.—Trapping effort for the microhabitat transects for each studied community.

Forest type	Year	Trapnights	Captures	Success rate
TSDF	All	11260	633	5.62
	2001	2980	73	2.45
	2002	3720	173	4.65
	2003	4560	387	8.49
CF	All	3620	315	8.70
	2001	1740	146	8.39
	2002	1880	163	8.67

harder to interpret but I included them since they accounted for >5 % of the total variance among trap stations. A graphic portrayal of the relationship between the first two factor scores showed separation between some species in their microhabitat use but also substantial overlap existed between other species (Figure 12). *Peromyscus pectoralis* showed a trend to separate from the rest of the species by leaning towards positive values of Factor 1. This species had the widest range of microhabitat use, being absent only from the open areas with the lowest values of canopy cover at the TSDF. On the other end of this factor range *Baiomys taylori* and *Sigmodon hispidus* made a tighter cluster in open grassy areas with the lowest values of canopy cover and tree density. Both *Oryzomys couesi* and *Liomys irroratus* showed some dispersion but both tracked the negative values of Factor 2 thus indicating a tendency towards sites with

Table 14.—Trapping results by species for the TSDF community. Abbreviations are: TC, total number of captures; TI, total number of individuals; MDC, number of individuals with microhabitat data.

Species	All Years			2001			2002			2003		
	TC	TI	MDC	TC	TI	MDC	TC	TI	MDC	TC	TI	MDC
Peromyscus pectoralis	325	136	120	34	20	13	75	31	28	216	85	79
Sigmodon hispidus	137	64	51	6	4	4	45	23	15	86	37	32
Liomys irroratus	74	48	44	18	17	16	31	17	15	25	14	13
Oryzomys couesi	53	38	37	10	10	10	8	8	7	35	20	20
Baiomys taylori	28	24	23	5	5	5	11	9	8	12	10	10
Oligoryzomys fulvescens	8	8	8	0	0	0	2	2	2	6	6	6
Rattus sp.	3	3	1	0	0	0	0	0	0	3	3	1
Mus musculus	2	2	0	0	0	0	1	0	0	1	0	0
Oryzomys rostratus	1	1	1	0	0	0	0	0	0	1	1	1
Reithrodontomys megalotis	1	1	1	0	0	0	0	0	0	1	1	1
Reithrodontomys mexicanus	1	1	1	0	0	0	0	0	0	1	1	1

Table 15.—Trapping results by species for the CF community. Abbreviations are: TC, total number of captures; TI, total number of individuals; MDC, number of individuals with microhabitat data.

Species	All Years			2001			2002		
	TC	TI	MDC	TC	TI	MDC	TC	TI	MDC
Peromyscus levipes	165	128	73	55	48	43	107	79	30
Peromyscus ochraventer	131	92	64	83	61	54	47	30	10
Oryzomys chapmani	11	11	9	5	5	5	4	4	4
Cryptotis mexicana obscura	4	4	3	2	2	1	2	2	2
Reithrodontomys mexicanus	1	1	1	1	1	1	0	0	0
Oligoryzomys fulvescens	1	1	1	0	0	0	1	1	1
Sorex saussurei	1	1	1	0	0	0	1	1	1

Table 16.—Number of total captures and total individuals from the vertical trapping transects. See text for details of how these transects were set.

Forest	Species	Total captures		total individuals	
		canopy	floor	canopy	floor
CF	*P. levipes*	81	51	50	28
CF	*P. ochraventer*	20	20	14	13
CF	*O. chapmani*	0	3	0	3
CF	*R. mexicanus*	2	0	2	0
CF	*C. mexicana*	0	3	0	3
TSDF	*P. pectoralis*	75	53	39	31
TSDF	*R. fulvescens*	1	0	1	0
TSDF	*O. couesi*	0	2	0	2

high shrub density values.

In contrast to the TSDF data, the correlations between variables was low for the CF dataset. An initial analysis that included all eleven variables showed poor measure of sampling adequacy for the overall dataset (KMO statistic < 0.5) and very poor values for many individual variables. The KMO statistic varies between 0 and 1, with low values of this statistic indicating diffusion in the pattern of correlations and hence non-appropriateness of a PCA approach (Field 2000). Thus, I progressively eliminated

Table 17.—Principal component factor scores and overall results of vegetation analysis for the Tropical Subdeciduous Forest community.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Canopy cover	0.359	-0.114	-0.081	-0.172	-0.091	0.389
Tree density	0.319	0.017	-0.162	0.003	-0.467	-0.476
Shrub density	0.156	-0.436	0.141	0.785	0.186	-0.238
Number of logs	0.135	0.276	-0.831	0.359	0.067	0.230
Litter density	0.352	-0.022	0.104	0.048	0.007	-0.034
Bare soil %	0.324	-0.403	-0.193	-0.317	-0.015	-0.181
Vascular plants %	-0.409	0.081	0.055	0.187	0.046	0.148
Large rocks %	0.303	0.480	0.211	0.133	-0.117	0.009
Shrub cover %	0.317	-0.252	0.218	0.075	0.012	0.643
Rocky outcrop distance	-0.265	-0.187	0.005	0.199	-0.841	0.207
slope	0.261	0.471	0.336	0.158	-0.100	-0.009
Eigenvalue	5.1391	1.4025	0.9378	0.8404	0.688	0.5653
Percent variation	0.467	0.128	0.085	0.076	0.063	0.051
Cumulative variation	0.467	0.595	0.680	0.756	0.819	0.870

variables, one at a time, based on the lowest values of sampling adequacy. Each time I ran the test again and verified the KMO value. After eliminating four variables an adequate level of the KMO statistic was reached (> 0.7). The final dataset included seven variables: canopy cover, tree density, shrub density, number of logs, litter density, percentage of bare soil and percentage of vascular plants. These correspond to variables one to seven from Table 12. For this CF restricted dataset the first five axes extracted by the PCA accounted for 92.4% of the variance in microhabitat structure among successful trap locations (Table 18). Tests indicated the appropriateness of a PCA approach for this

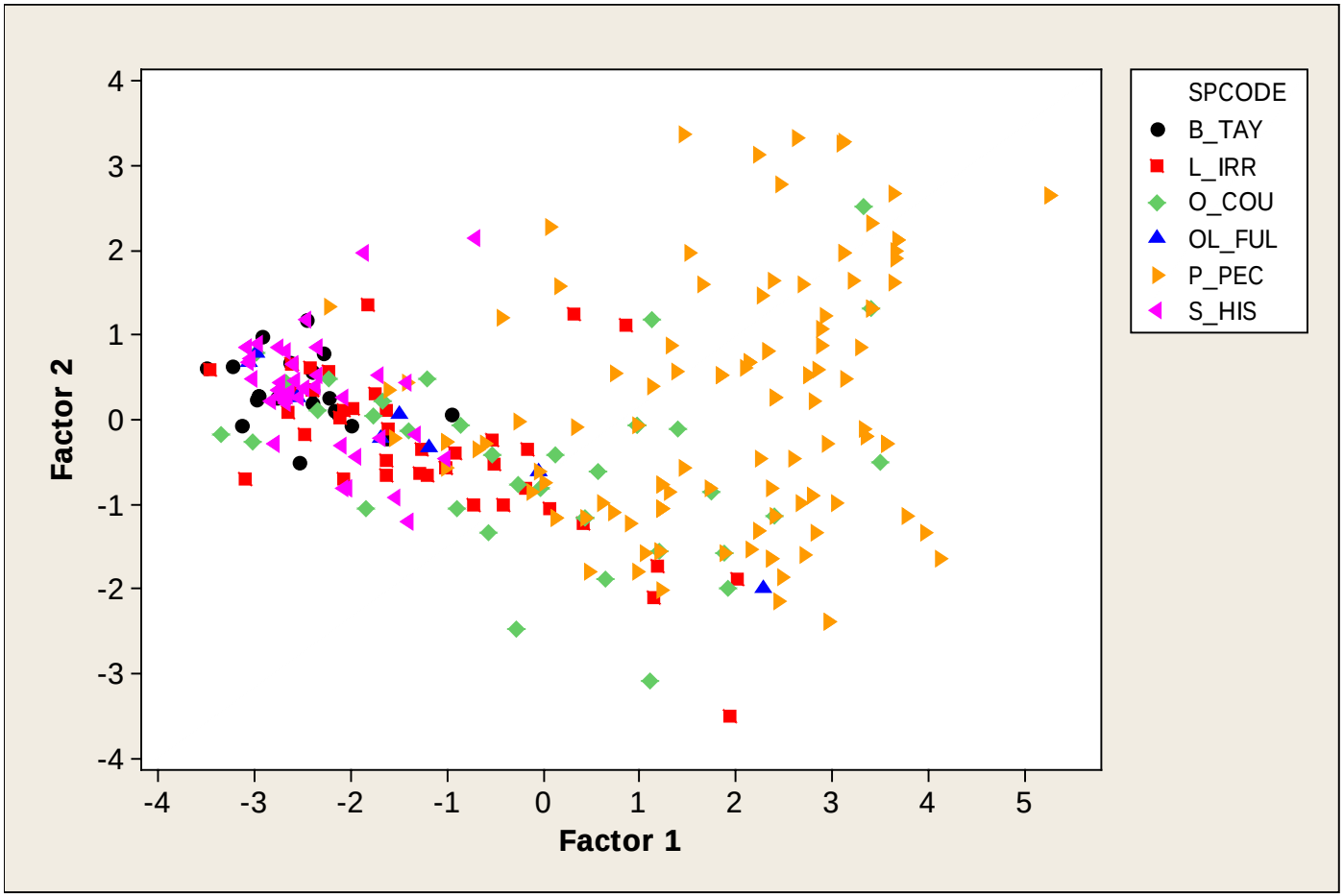

Figure 12.—Principal Component Analysis ordination showing species microhabitat use in the TSDF assemblage. The first and second axis accounted for 46.7% and 12.8% of the total variance among trap locations, respectively. Species abbreviations as in Appendix II.

reduced dataset (KMO measure of sampling adequacy = 0.724, Bartlett's test of sphericity = 336.979, P<0.0001). Species present at this vegetation type did not show any evident separation of microhabitat use (Figure 13), and all four species of small mammals have a trend towards negative values of Factor 2. This Factor separated trap stations with large amounts of bare soil against stations with high amounts of fallen logs and stumps around it.

For both forests I saved as new variables these factor scores for the first six (TSDF) and five (CF) principal components and calculated a mean value for each one. I used these mean values to perform a cluster analysis that showed four distinctive clusters for the TSDF species (Figure 14) and three for the CF species (Figure 15). This cluster analysis, together with the results of temporal niche analyses, served as guides to generate specific tests between species or groups. For the TSDF I did the following tests: *B. taylori* against *S. hispidus* (cluster A), *L. irroratus* against *O. fulvescens* (cluster B), cluster A against cluster B, cluster B against *O. couesi* and *P. pectoralis* against the rest of the species. For the CF, the dendogram showed three clusters but all species in this vegetation type also showed strong overlap in the ordination chart (Figure 13). So, tests for differences between them comprehended only three relevant comparisons: between all species, between both *Peromyscus* species and between the *Peromyscus* cluster and the rest of the species. All MANOVAs for both vegetation types yielded an overall low correlations for residuals (< 0.5) so there was not much support that a multivariate analysis was more appropriate than a set of individual univariate tests (ANOVA) for each variable and thus I report these also.

Table 18.—Principal component factor scores and overall results of vegetation analysis for the Cloud Forest community.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Canopy cover	-0.471	0.026	0.11	0.213	-0.393
Tree density	-0.319	0.167	0.306	0.749	0.382
Shrub density	0.244	0.065	-0.805	0.483	-0.026
Number of logs	-0.145	0.908	-0.111	-0.289	0.204
Litter density	-0.444	0.095	-0.187	-0.01	-0.642
Bare soil %	-0.439	-0.174	-0.426	-0.171	0.336
Vascular plants %	0.454	0.323	0.133	0.22	-0.363
Eigenvalue	3.1341	1.0015	0.9282	0.8199	0.5842
Percent variation	0.448	0.143	0.133	0.117	0.083
Cumulative variation	0.448	0.591	0.723	0.841	0.924

Both parametric and non-parametric tests of the complementary set of variables yielded consistent results for the TSDF tests (Table 19 and 20). I found no differences between either the species that form cluster A or cluster B for any of the microhabitat variables. However, several differences between clusters existed in terms of tree density, shrub density, canopy cover, percentage of bare soil and percentage of vascular plants. For the rest of the variables these clusters had no differences. The contrast of *O. couesi* against cluster B, which includes *L. irroratus,* showed that for the eleven variables only four were different (Tree density, canopy cover, percentage of large rocks and slope) with two being marginally different (tree density and canopy cover). So,

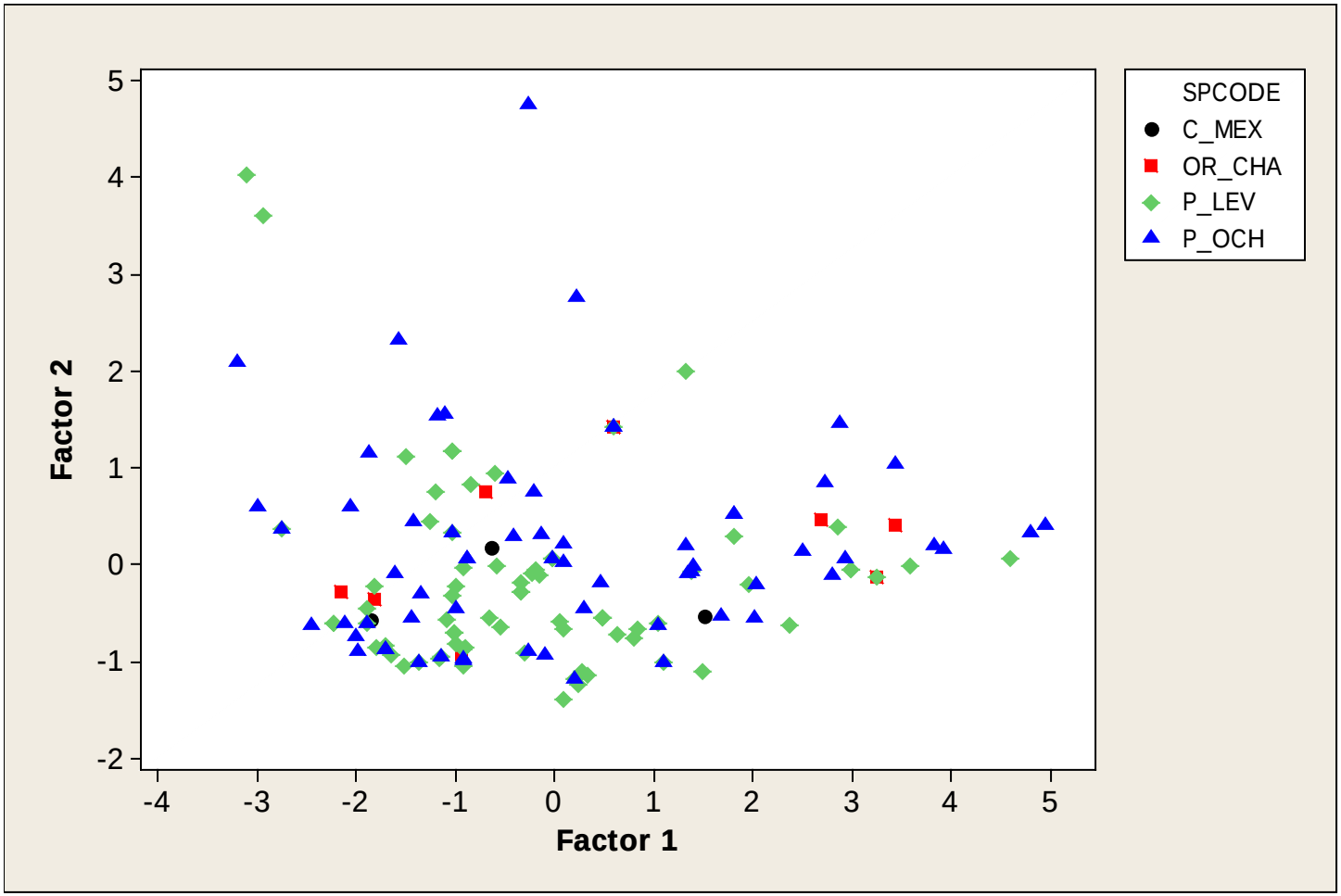

Figure 13.—Principal Component Analysis ordination showing species microhabitat use in the CF assemblage. The first and second axis accounted for 44.8% and 14.3% of the total variance among trap locations, respectively. Species abbreviations as in Appendix II (plus: C_MEX = *Cryptotis mexicana*).

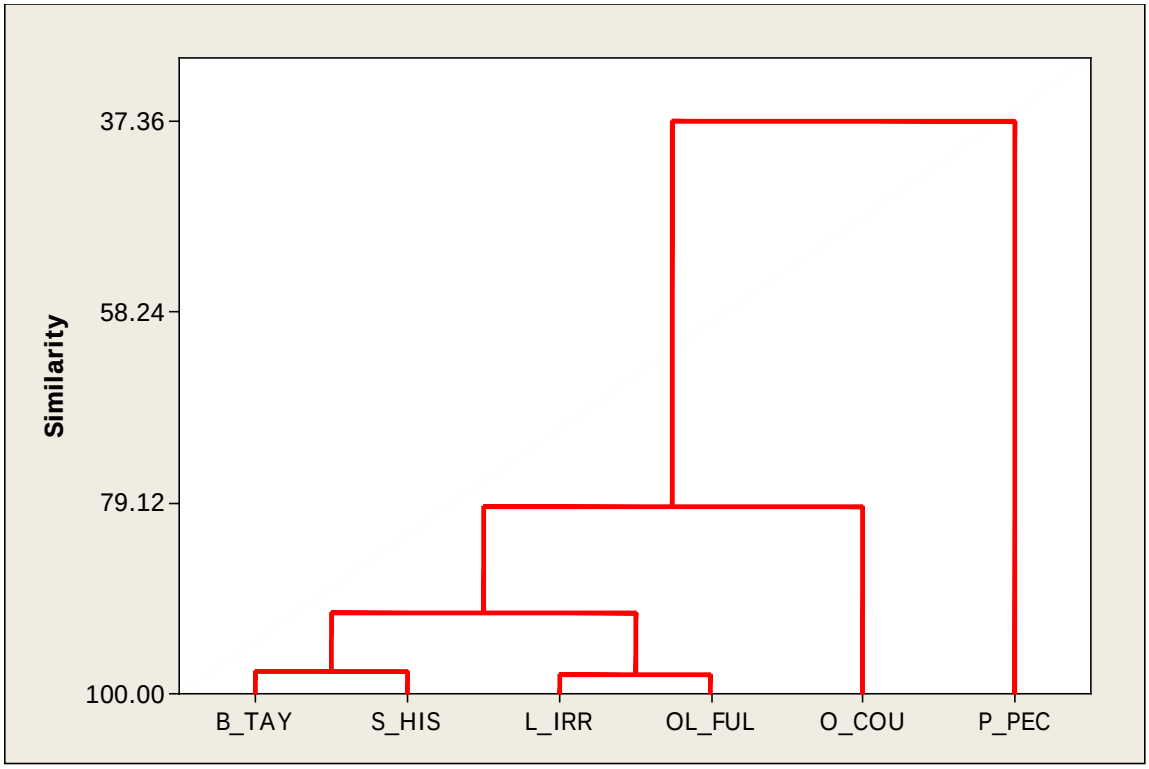

Figure 14.— Dendogram of microhabitat niche similarities for the most abundant rodent species of the TSDF assemblage. Species abbreviations as in Appendix II.

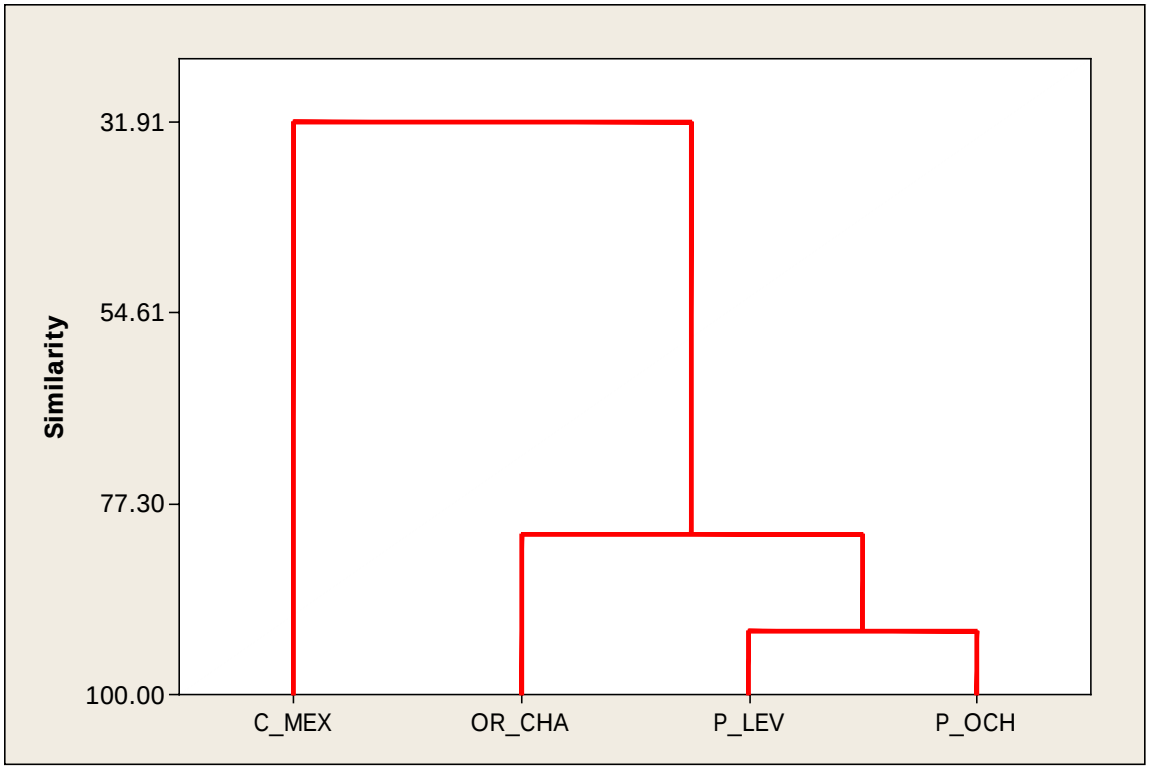

Figure 15.— Dendogram of microhabitat niche similarities for the most abundant rodent species of the CF assemblage. Species abbreviations as in Appendix II.

Table 19.—Results of MANOVA for normal microhabitat variables between selected species and group pairs from the TSDF assemblage. P values are from Wilks' Lambda. Abbreviations are: TD, tree density; SD, shrub density; NL, number of logs; DRO, distance to rocky outcrop; SLO, slope. A description of these microhabitat variables is in Table 12.

		MANOVA		ANOVA	
Group/species comparison	Variables	F	P	F	P
B. taylori vs *S. hispidus*		1.654	0.158		
	TD			1.83	0.18
	SD			0.5	0.48
	NL			0.69	0.48
	DRO			2.7	0.11
	SLO			1.23	0.27
L. irroratus vs *O. fulvescens*		0.876	0.5		
	TD			0.25	0.62
	SD			1.61	0.21
	NL			0.04	0.85
	DRO			0.23	0.64
	SLO			0.37	0.55
Cluster A vs cluster B		6.231	<0.0001		
	TD			23.21	<0.001
	SD			3.83	0.05
	NL			0.47	0.50
	DRO			0.98	0.23
	SLO			1.95	0.17
Cluster B vs *O. couesi*		2.046	0.08		
	TD			4.03	0.05
	SD			1.40	0.24
	NL			2.83	0.10
	DRO			3.22	0.08
	SLO			6.62	0.01
P. pectoralis vs rest of spp		75.48	<0.0001		
	TD			184.05	<0.001
	SD			41.14	<0.001
	NL			22.28	<0.001
	DRO			269.92	<0.001
	SLO			59.95	<0.001

Table 20.—Results of Mann-Whitney tests for non-normal microhabitat variables between selected species and group pairs from the TSDF assemblage. Abbreviations are: CPC, canopy cover; LTD, litter density; PBS, % bare soil; PVP, % vascular plants; PLR, % large rocks; PSC, percentage shrub cover. Variables are described in Table 12.

Group/species comparison	Variables	U	P
B. taylori vs *S. hispidus*	CPC	573.5	0.88
	LTD	541.5	0.55
	PBS	571	0.86
	PVP	568	0.83
	PLR	580	0.90
	PSC	217.5	0.37
L. irroratus vs *O. fulvescens*	CPC	167	0.83
	LTD	151	0.54
	PBS	175	0.99
	PVP	173	0.95
	PLR	144	0.43
	PSC	151	0.54
Cluster A vs cluster B	CPC	812	<0.001
	LTD	1778	0.42
	PBS	1487.5	0.03
	PVP	1529	0.05
	PLR	1881.5	0.73
	PSC	1090	<0.001
Cluster B vs *O. couesi*	CPC	485.5	0.05
	LTD	569.5	0.26
	PBS	549.5	0.20
	PVP	506.5	0.08
	PLR	461.5	0.03
	PSC	531.5	0.14
P. pectoralis vs rest of spp	CPC	2990.5	<0.001
	LTD	3349	<0.001
	PBS	3603.5	<0.001
	PVP	1939.5	<0.001
	PLR	4044	<0.001
	PSC	4727	<0.001

overall these species use highly similar microhabitats located over ecotonal areas with O. couesi having a tendency towards zones inside the closed forest, thus the reason cluster analysis grouped it separately. Lastly, *P. pectoralis* had highly significant differences from the rest of the species in all the microhabitat variables measured.

The CF community had contrasting results against the TSDF assemblage. When all species are compared I found no significant differences at the multivariate level ($F = 1.42$, $P = 0.2$), and the univariate level for both of the normal variables tested (tree density, $F = 0.13$, $P = 0.94$; shrub density, $F = 2.44$, $P = 0.07$). Additionally, the Kruskal-Wallis test showed the same result for the rest of the variables (canopy cover, $X^2 = 1.34$, $P = .719$; number of logs, $X^2 = 1.23$, $P = .746$; litter density, $X^2 = 3.63$, $P = .305$; percentage of bare soil, $X^2 = 6.48$, $P = 0.09$) except for one variable that exhibited differences between all species at this assemblage (percentage of vascular plants, $X^2 = 10.78$, $P = 0.01$). When I compare the cluster formed by both *Peromyscus* species at this forest I obtain the same outcome of no differences in the microhabitat variables except for the percentage of vascular plants (Mann-Whitney $U = 1639$, $P = 0.002$). The last comparison, between the Peromyscus cluster and the rest of the species showed that they use the same microhabitat variables. This includes all normal variables at both the multivariate ($F = 1.31$, $P = 0.32$) and univariate level (tree density, $F = 0.15$, $P = 0.7$; shrub density, $F = 2.28$, $P = 0.13$) as well as the rest of the variables (canopy cover, $U = 739$, $P = .563$; number of logs, $U = 796.5$, $P = .84$; litter density, $U = 818$, $P = .97$; percentage of bare soil, $U = 625.5$, $P = .17$).

Scansorial activity analysis.— The vertical transects detected three species in the TSDF and five in the CF (Table 16). Of these, only the *Peromyscus* species had enough captures to conduct analyses. At the CF, I found no differences between the number of captures at floor and vegetation layer traps for the syntopic pair of *Peromyscus* for either total number of captures (X^2 = 1.635, d.f.=1, P = 0.2) or total number of individuals (X^2 = 1.265, d.f.=1, P = 0.26). Both species had no differences against the null hypothesis of equal use of floor and vegetation layers. This pattern was very clear for *P. ochraventer* for all first captures (X^2 =0.019, d.f=1, P =0.9) and even the total number of captures was exactly the same (Table 16). But for *P. levipes* this pattern was marginally non-significant for both the first captures (X^2 =3.16, d.f.=1, P = 0.07) and all captures (X^2 = 3.45,d.f.=1, P = 0.06) with a tendency towards more scansorial activity. In the TSDF only *P. pectoralis* had enough captures to do an analysis. I found no support to reject the hypothesis of an equal use of floor and vegetation layers in this species for either first captures (X^2 = 0.46,d.f.=1, P =0.5) or total number of captures (X^2 =1.9, d.f.=1, P = 0.16).

DISCUSSION

Overall the two communities show contrasting results. These assemblages not only differed in their species richness but also in the relative abundance patterns, separation among microhabitats, and trapping success ratios.

The was a large between-year increase for the trapping success at the TSDF compared to the more constant ratios at the CF. In 2001 very few individuals were captured in the

TSDF compared to 2003. Even after correcting for differences in trapping effort, the success ratio was 3 times higher in 2003. This possibly reflects effects that hurricane Keith had on the rodent populations at the TSDF. This hurricane hit directly over the reserve zone in October of 2000, causing numerous tree falls and extensive flooding in the lower-laying zones. This area of the Sierra Madre Oriental has a high incidence of natural disturbances caused by these hurricanes, and as such they have had a high impact in forest dynamics over long time scales (Arriaga 1987; Valiente-Banuet et al. 1995). Unfortunately, no rodent surveys at the TSDF were done before October 2000, so it is impossible to assess the exact impact this disturbance had on rodent populations at TSDF. Why the rodent populations at the CF were seemingly not affected by this disturbance is unknown.

Microhabitat use analyses portray different small mammal community dynamics for each forest. At the TSDF I found a structured assemblage where species divided into smaller groups that specialized in different microhabitats whereas in the CF no substantial differences in microhabitat use occur between present species. At the TSDF separation was not complete and some overlap existed between species or groups. In general, available microhabitats at the TSDF represented a gradient that goes from open stations to closed forest trap stations. Open areas were flat, grassy zones that had few trees, no leaf litter and no rocky boulders. The other extreme of the gradient had high values of canopy cover, tree density and leaf litter. Additionally, this zone had large boulders, fallen logs or stumps and inclined slopes, since closed forest areas occurred mostly on hillsides. The ecotone zone between these two extremes distinguished itself

by a higher shrub density than any of the other areas. Species were divided along this gradient with *S. hispidus* and *B. taylori* occurring mostly in the grassy and completely open areas with no canopy cover. This species pair co-occurs widely in the grassland type habitats of Texas like the Coastal Prairie (Joule and Cameron 1980; Baker 1991), the Grand Prairie of the north-central region of the state (Hanchey and Wilkins 1998), and the Post-oak Savanna (Turner and Grant 1987). In these habitats they overlap widely in their microhabitat use and generally *S. hispidus* is a more abundant and dominant species (Eshelman and Cameron 1987). At the coastal prairie study site *S. hispidus* was a codominant species, together with *R. fulvescens,* with *B. taylori* appearing only seasonally. There is evidence both in laboratory (Putera and Grant 1985) and field studies (Raun and Wilks 1964; Schmidly 1983) that agonistic interactions shape competition between these two rodents. At my study sites this species pair not only shared the same microhabitat but also had the highest overlap in temporal activity since both are mainly crepuscular species (Chapter III). At the same time they had the largest difference in body mass of all members of the TSDF assemblage (Appendix II). It has been suggested that differences in body sizes reduce competition and promote local coexistence. For desert rodents from southwest North America, it has been shown repeatedly that species which coexist in local habitats are highly non-random assemblages with respect to body size (Bowers and Brown 1982; Brown 1973; Hopf and Brown 1986). Wether the large difference in body size between *S. hispidus* and B. *taylori* represent a non-random pattern or just a chance convergence of two species in this microhabitat remains an open question.

Other species that used open microhabitats, at least partially, were three species with neotropical origins: *L. irroratus, O. fulvescens and O. couesi.* Although all three were captured in some traps stations at relatively open microhabitats, they differed from the previous species pair because they tended towards ecotonal areas that had higher shrub densities and some canopy cover. Within this group *O. couesi* showed more tendency towards zones with the highest density of shrubs that represent the forest borders, but overlapped greatly with the other two species. Through its range *L. irroratus* normally occupies steppe, thicket and scrub type vegetation as well as subtropical palm forests and prickly pear thickets (Davis and Schmidly 1994; Dowler and Genoways 1978). It occurs widely in the Tamaulipas coastal plain (Alvarez 1963) and the Mexican central plateau (Dowler and Genoways 1978). At ECBR it occurs on the xeric habitats on the western slopes of the Sierra Madre Oriental but is absent from the more mesic areas of the reserve. *O. fulvescens* is clearly an ecotonal species that favors deciduous forest edges, secondary growth and tall grasses (Reid 1997). This species is also present in the CF and xeric scrub vegetation zones (Chapter II). *O. couesi* has been reported in shrubby habitat along the edges of open grassy fields (Villa and Cervantes 2003) as well as in cattail marshes and grassy zones near oxbow lakes (Davis and Schmidly 1994). At ECBR this species is restricted to the TSDF vegetation type (Chapter II).

Worth noting between the species pair of *O. couesi* and *L. irroratus* is their highly similar body mass (Appendix II) and their completely opposite activity pattern (Chapter III). The niche complementarity exhibited by this species pair is opposite to

the one exhibited by the open area species. Reappearance of these kinds of patterns within the same assemblage deserves further inquiry since it seems unlikely that all could be explained by chance convergences.

The most abundant species at the TSDF sites, *P. pectoralis*, was also the species that occupied the most distinct microhabitat type, located inside the closed forest zones. All ecotone species had at least one capture inside the forest but the numerically dominant species at these trap stations was clearly *P. pectoralis*. In Texas this species is considered a rock-dwelling species commonly associated with this substrate in oak-juniper woodlands (Davis and Schmidly 1994), being most abundant in association with slopes and limestone outcrops (Etheredge et al. 1989; Hanchey and Wilkins 1998). In Tamaulipas it has been detected in rocky slopes with low brush (Hooper 1952), riparian forests, deciduous thickets and thorn woodlands (Schmidly and Hendricks 1984). At the TSDF sites the closed forest trap stations were highly correlated with ascending slopes and increasing rockiness. Given the close association that exists between forest density and rocky substrate in the data from my study sites it is impossible to tease out which variable is more relevant to the occurrence of this species. However, evidence from other localities points towards the higher importance of a rocky substrate for the presence of *P. pectoralis* (Schmidly 1977; Schmidly and Hendricks 1984; Geluso 2004). Relevant also to the understanding of the numerical dominance of this species is the heavy use of the vertical layer by *P. pectoralis*. Vertical trapping transects showed that this species used the vegetation layer as much as the floor. Semi-arboreal behavior has been reported for several species of *Peromyscus* including *P. pectoralis* (Holbrook 1979;

Barry et al. 1984; Mullican and Baccus 1990; Laakkonen 2003). At the TSDF *P. pectoralis* not only dominated the use of the forest trap stations but alone among other species used the vertical vegetation layer. Use of this layer presumably allows this species to reach other resources not used by the rest of the species thus giving it an advantage to increase local abundance. Other studies have shown that in assemblages where rodents present arboreal/scansorial activity abundance estimates will be biased if only floor traps are used (Laakkonen 2003). The lack of difference between the number of individuals caught in ground vs. vertical traps and the higher success ratio in the vertical transects of my study confirms the need to integrate this kind of trapping at sites where vertical structure is present. Vertical transects not only will aid in gathering more accurate density information but also can aid to detect rare species. *Reithrodontomys fulvescens* was the only other species using this vertical structure. I detected a single individual that represents the only record for the entire study (see Chapter II). Interestingly, at the coastal zone sites in Texas of mostly grassland habitat, this species is the co-dominant member of the rodent community, together with *S. hispidus* (Kincaid et al. 1983), but at the TSDF it is an extremely rare species occurring only in vertical forest microhabitat.

Overall, patterns of microhabitat use at TSDF sites are highly concordant with what has been observed in other localities for each species (Kincaid et al. 1983; Turner and Grant 1987; Hanchey and Wilkins 1998). Differences between species were significant but not enough to yield a complete separation. Observed overlap shows that for all species some individuals use microhabitats to some extent, where other species

are more abundant. Thus, some interactions between individuals of all species present is likely. Whether differences in microhabitat use are due to phylogenetic constraints (microhabitat selection) or species interactions (competition, predation) is a question resolved only by two complementary approaches: experimental manipulations (Bowers et al. 1987; Abramsky et al. 1990; Brown 1998) and inclusion of historical data (Losos 1996). The seemingly elaborate structure present at the TSDF assemblage should not be surprising given that a much more simple environment like the desert regions of south western North America harbor diverse and intricately organized assemblages of rodents (Brown and Harney 1993).

Contrasting heavily with the TSDF assemblage, the small mammal community at the CF exhibited little structure. Diversity at these sites was lower, with the community being co-dominated by the pair of *Peromyscus* species that occur at this vegetation type. Microhabitat transects showed that no major differences existed between species for almost all variables I measured. Only one floor cover variable, ie. ground vascular plant cover, presented differences between the two co-dominant *Peromyscus* species. In addition, this species pair presented no differences in their activity patterns (Chapter III) and use of vertical structure, though sample sizes were low. When the number of captures for each species was tested separately against the null hypothesis of equal number of captures between floor and vegetation layer traps the results are only marginally non-significant for *P. levipes*. Adding only a single canopy capture to this analysis would have made the difference significant, indicating a likely higher use of the vegetation layer by this species. Interspecific differences in arboreal activity of rodents

has been proposed as a mechanism of species coexistence (Laakkonen 2003) but no experimental test of this idea has been attained. Given the strong co-dominance of this species pair at the CF, this assemblage presents an adequate setting to attempt this test. Similarly, the relative importance of plant ground cover for coexistence of this pair of species presents a task amenable for experimental testing. Manipulative experiments of ground cover and species removal will provide a definitive answer for both hypotheses.

A niche axis not addressed in my study, ie. food, is potentially important for ecological separation in this species pair and should be addressed to assess its role. Another possible explanation for the lack of strong separation for the niche axes I addressed might be due to the difference in body size between *P. levipes* and *P. ochraventer*. The ratio between them is modest (1.5) but nevertheless within the range of observed differences between coexisting rodent species (Bowers and Brown 1982). More important than the ratio itself is the issue of whether this difference is due to a species sorting mechanism or just random sorting of this species pair. Analysis of other assemblages where these species occur might be able to answer this.

The striking disparity between the small mammal communities at the two forests I studied are likely due to a combination of their different physiognomy (August 1983) and colonizing pools of species (Alvarez 1963). The CF lacks grassland microhabitats and thus species highly associated with them. Also, this forest has no sharp ecotones and its boundaries with the major vegetation types it abuts are gradual. Recent research of ecotones, particularly those between savannas and rain forests, suggest they might be important sources of speciation (Smith et al 1997). These ideas remark the need for

studies that address the role of historical effects for rodent assemblages at ECBR. Detailed histories of species colonization patterns will likely give insight to explain the differences between these forests. Without this knowledge ecological studies can only provide a partial picture of the complexity of these unique assemblages.

Basic studies of animal community patterns from ECBR are almost nonexistent thus preventing further inquiry on the ultimate processes that have shaped the high species diversity present at this zone. Undoubtedly, the highly heterogeneous terrain and the geographic location of the reserve over a convergence zone of temperate and tropical biomes have had profound roles in the creation of this diversity (Schluter and Ricklefs 1993). The fact that large numbers of species occur at this zone is known (Martin 1955; Martin 1958; Vargas-Contreras and Hernandez-Huerta 2001) but we lack the information on their organization and the ultimate processes related to this diversity. As a first step towards that ultimate goal my study provides the first detailed account of the small mammal community structure from ECBR.

CHAPTER V

SUMMARY

Given the unique nature of ECBR as a convergence zone of tropical and temperate biomes it provides a unique scenario for studying mechanisms of community assembly, landscape ecology and evolutionary processes. My study provides evidence that rodent communities at this zone can be highly structured assemblages at different spatial scales. This has been demonstrated for desert rodent communities (Brown et al. 2000; Brown et al. 2002) that occur over large spans of relatively uniform habitat, but not for communities over major biome contact zones. Using recent analytical advances of community structure I show proof of non-random patterns at the landscape and local level for ECBR rodent communities. I detected large differences in species diversity, species composition and overall structure in the rodent assemblages between two adjacent forest types, TSDF and CF, from the eastern slope gradient of ECBR. Null model analyses provided evidence that rodent species were not randomly distributed along this gradient, this especially true for abundant mid-sized species that include those from the genus *Peromyscus*. Highly similar patterns of segregation of *Peromyscus*, including some species present at ECBR, are repeated over other mountain ranges in Tamaulipas, New Mexico and Texas (Alvarez 1963; Schmidly 1977; Schmidly and Hendricks 1984; Geluso 2004) but none have been rigorously tested using null model or multivariate approaches. Scant phylogenetic data suggest related species replace each other within mountain ranges at similar elevation and habitat types. This will require the generation of complete genealogies to assess the role of this historical data on

community assembly. The non random species distribution patterns I have shown for ECBR are not specific to this zone but form part of a larger pattern that repeats itself over the mountains of eastern Mexico and south-central USA. This evidence is suggestive that species interactions might have an important role in the creation of distribution patterns along elevational gradients, however there is a need to include historical data as part of the analysis as well.

Additionally, patterns at the landscape scale will not be elucidated unless we understand how interactions between populations of rodent species allow for the coexistence of ten rodent species at the TSDF against five from the CF. Parts of my study that addressed species patterns at local scales give some insights into this question. Structural differences between each forest provide a partial answer to the difference in species numbers since the presence of additional microhabitats at the TSDF harbors species not found at the CF. Furthermore, I showed that the TSDF had a more structured community where the interplay of temporal patterns, spatial use and morphological species features, i.e. body mass, very likely allows for the coexistence of this larger number of species. At the TSDF species were organized along a microhabitat gradient that spans open-grassy areas to closed forest zones. The whole community partitions time in a non-random fashion, with species from ecotone/open areas avoiding use of middle portions of the night whereas the single forest species concentrated activity at this period.

In sharp contrast the CF community, codominated by two *Peromyscus* species, overlapped heavily in both their microhabitat use and diel activity patterns. Ecological

separation of these two species probably occurs along a niche axis not considered in my study or might be facilitated by their body mass difference. Overall, I provide the first rigorous and detailed account of community patterns for small mammals at ECBR, which will provide a strong foundation for the design of experimental manipulations aimed to ascertain mechanisms responsible for structure at these communities.

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APPENDIX I

List of *Peromyscus* individuals, and GenBank accession numbers, used as reference for genetic identification analyses. Information for these specimens was taken from related published articles (Bradley, Tiemann-Boege, Kilpatrick, and Schmidly 2000; Tiemann-Boege, Kilpatrick, Schmidly, and Bradley 2000).

Peromyscus levipes ambiguus

México: Nuevo Leon, Cola de Caballo (AF131928).

Peromyscus levipes levipes

México: Tlaxcala, 2 Km W Teacalco (AF131929).

México: Queretaro, 8.2 mi N, 1.8 mi W Amealco (AF155396).

Peromyscus pectoralis laceianus

USA: Texas, Kimble Co., Walter Buck Wildlife Management Area (AF155400).

Peromyscus pectoralis pectoralis

Mexico: Durango, 1.5 Km SE Las Herreras, 1694 m (AF155401).

Sequences of primers utilized in PCR and DNA sequencing protocols.

Primer	Nucleotide sequence (5' - 3')
MVZ05	CGAAGCTTGATATGAAAAACCATCGTTG
752R	GCAGGAGTGTAATTATCGGGGTCTC
P3'	TCTCTCCGGTTTACAAGACCAAGGT
766R	GTTTAATTAGAATTAGCTTTGGG
765F	GAAAAACCACGTTGTATTCAACT

APPENDIX II

Species distribution among the habitat types sampled at ECBR during 2001 to 2003.

Family	Subfamily	Species	Species Abreviation	body mass (g)	body mass guild	CF	TS	TSDF	CPV
Heteromyidae	Heteromyinae	*Liomys irroratus*	L_irr	39.13	medium	0	0	1	1
Muridae	Sigmodontinae	*Baiomys taylori*	B_tay	8.06	small	0	0	1	1
Muridae	Sigmodontinae	*Oligoryzomys fulvescens*	Ol_fulv	12.25	small	1	1	1	1
Muridae	Sigmodontinae	*Oryzomys chapmani*	Or_cha	28.00	medium	1	1	0	0
Muridae	Sigmodontinae	*Oryzomys couesi*	Or_cou	36.48	medium	0	0	1	0
Muridae	Sigmodontinae	*Oryzomys rostratus*	Or_ros	34.00	medium	0	0	1	0
Muridae	Sigmodontinae	*Peromyscus leucopus*	P_leu	18.50	medium	0	0	0	1
Muridae	Sigmodontinae	*Peromyscus levipes*	P_lev	25.93	medium	1	1	0	0
Muridae	Sigmodontinae	*Peromyscus ochraventer*	P_och	33.59	medium	1	1	0	0
Muridae	Sigmodontinae	*Peromyscus pectoralis*	P_pec	23.17	medium	0	0	1	0
Muridae	Sigmodontinae	*Reithrodontomys fulvescens*	R_fulv	11.50	small	0	0	1	0
Muridae	Sigmodontinae	*Reithrodontomys megalotis*	R_meg	9.00	small	0	0	1	0
Muridae	Sigmodontinae	*Reithrodontomys mexicanus*	R_mex	13.33	small	1	1	1	0
Muridae	Sigmodontinae	*Sigmodon hispidus*	S_his	53.21	large	0	0	1	1

Species distribution sensu Vargas-Contreras and Hernandez-Huerta (2001).

FAMILY	SUBFAMILY	SPECIES	TSDF	CF	OPF	XS
Heteromyidae	Dipodomyinae	*Dipodomys ordii*	0	0	0	1
Heteromyidae	Perognathinae	*Chaetodipus nelsoni*	0	0	0	1
Heteromyidae	Heteromyinae	*Liomys irroratus*	1	0	0	1
Muridae	Sigmodontinae	*Neotoma albigula*	0	0	0	1
Muridae	Sigmodontinae	*Neotoma angustapalata*	0	1	0	0
Muridae	Sigmodontinae	*Baiomys taylori*	1	0	0	1
Muridae	Sigmodontinae	*Oligoryzomys fulvescens*	1	1	0	1
Muridae	Sigmodontinae	*Onychomys arenicola*	0	0	0	1
Muridae	Sigmodontinae	*Oryzomys chapmani*	0	1	0	0
Muridae	Sigmodontinae	*Oryzomys couesi*	1	0	0	0
Muridae	Sigmodontinae	*Oryzomys rostratus*	1	0	0	0
Muridae	Sigmodontinae	*Peromyscus leucopus*	1	0	0	1
Muridae	Sigmodontinae	*Peromyscus levipes*	1	1	1	0
Muridae	Sigmodontinae	*Peromyscus ochraventer*	1	1	1	0
Muridae	Sigmodontinae	*Peromyscus pectoralis*	1	1	1	1
Muridae	Sigmodontinae	*Reithrodontomys fulvescens*	1	0	0	1
Muridae	Sigmodontinae	*Reithrodontomys megalotis*	1	1	0	0
Muridae	Sigmodontinae	*Reithrodontomys mexicanus*	1	1	0	0
Muridae	Sigmodontinae	*Sigmodon hispidus*	1	1	0	1

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1995 Participant of the Research Training Program at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Publications

Castro-Arellano, I., H. Zarza and R. Medellin. 2000. *Philander opossum*. Mammalian Species, 638: 1-8.

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